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PRESIDENTIAL ADDRESS

MYCOLOGICAL CONTACTS

By R. W. MARSH, M.A.

This address will give some examples, taken mainly from personal experience, of the association of mycology with the studies included in agricultural research. The value of this association to the study of mycology and to the strength of this society is emphasized. A plea is made for corresponding associations with the medical and industrial fields touching mycology. Methods of promoting this end are briefly considered in relation to the general problem of the integration of the biological societies.

Mycology and agricultural science

It is possible for a government mycological service to stand detached from the general research and advisory service for agriculture. This happens, for example, in Canada, where a segregated Plant Pathological Service staffs a chain of laboratories in which not a solitary chemist or entomologist serves to leaven the mycological lump. But the usual British and United States system is one of association of mycologists with workers in other plant sciences in a research institute primarily established for an allied group of crops, as at Cheshunt, East Malling and Long Ashton. As the mycological service to agriculture expands, the question will undoubtedly arise whether this dispersal of mycologists shall continue or whether they should be grouped in an institute or institutes of plant pathology. There are obvious advantages in promoting the centralization of the legislative and regulatory branch of the service and of the fundamental investigations on fungicides. But in those aspects of mycology applied to agriculture that are now dealt with by the advisory and research mycologists, the proximity to other non-mycological workers gives valuable opportunities for co-operative investigations. Joint work is of great aid in arriving at balanced judgements.

The need for co-operation is apparent in plant-disease studies, where the field problems are invariably complex, their solution requiring assistance, on the biological side alone, from plant physiologists, chemists, soil scientists and entomologists. Where these workers are under the same roof, it is relatively easy for them to consult together and hammer out an agreed method of dealing with a plant pathological problem. This procedure is far more satisfactory to a grower than the alternative of leaving it to him to fit together the scattered bits of a solution of his problem as they arrive, first from one laboratory, then from another. In a plant-disease investigation it will often fall to the lot of the mycologist to assemble and present the unified conclusions of a group of workers. This is a very wholesome corrective of any one-sided approach to a question: an effective antidote to over-specialization.

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The study of the responses of plants to nutritional deficiencies is a rapidly extending zone in the environs of plant pathology but is not a domain to be termed mycological in the stricter sense. But the interaction of these nutritional factors with the expression of plant diseases caused by fungi opens up a wide field for joint investigations in plant physiology, pedology and mycology.

To quote from Dr Pethybridge's presidential address at Hereford in 1926, 'Although an enormous amount of work has been done on soils and manuring from a chemical point of view, very little of it has had any special bearing on plant pathology. It has often struck me that there is a field of work here for the pathologist well worthy of closer attention and one which might yield important and far-reaching results.' In considering this problem we have first the relatively straightforward examples, such as Club Root, where the degree of infection is largely determined by soil factors which may be modified by manurial applications, irrespective of the result of these applications on the plant. A more complex situation is exemplified by Mr Garrett's pot-culture work on the interactions between nutritional deficiency and *Ophiobolus* infection of wheat. He found, that in the absence of the fungus, deficiences of nitrogen and of potassium did not result in significant depression of yield compared with that from the full nutrient (NPK) series. Deficiency of phosphate, however, in itself greatly reduced yield. In a parallel series of pot cultures exposed to soil infection with *Ophiobolus*, root infection was least in the nitrogen-deficient plots and greatest in the phosphate-deficient, while the percentage infection of stem bases was lowest in the nitrogen-deficient and in the fully fed series. Comparing the infected plants with the controls, yield was reduced in every series except that receiving full nutrient. The greatest loss of yield due to disease was in the phosphate-deficient series, but significant reductions were also shown in the nitrogen- and potash-deficient infected cultures.

One reason that may be adduced for the accentuation of *Ophiobolus* attack by phosphate deficiency is that phosphate, more than any other fertilizer, encourages rooting. Plants with their root systems crippled by the Take-all fungus are able to produce fresh roots in phosphate-rich soil but cannot repair a loss of roots in soil where phosphate is lacking.

A further step takes us from the root-attacking fungi to those infecting only the above-ground portions of plants. A number of water-culture investigations and field trials have demonstrated that susceptibility to Mildew and Yellow Rust in wheat and to Mildew in barley was increased by heavy nitrogenous manuring and decreased by potash. In Chocolate Spot of beans, potash deficiency again is associated with increased liability to infection, and a team of workers at Wye has recently shown also that a highly significant relation exists between the resistance to attack in the field and the amount of available phosphate determined in the soil. A warning, however, against generalizing that phosphate deficiency and *Botrytis* attack always go hand-in-hand is afforded by the fact that *Botrytis* did not infect phosphate-deficient lettuce in pot culture experiments at Long Ashton but was most damaging in the calcium-deficient cultures.

Such results are not necessarily explicable on the assumption that a nutritional deficiency results in a weakly growing plant readily susceptible to disease. Apple Scab attack is reduced on the weakly growing trees kept short of nitrogen, although under orchard conditions there is the obvious complication that the tree making restricted growth has a less dense head of foliage than the fully fed tree and so dries more rapidly after rain. This, however, is not the sole factor concerned, as Muskett, Horne and Colhoun, working with Bramley's Seedling apples from Northern Ireland, have shown that nitrogenous manuring, with or without potash and phosphate, led to a marked increase in the nitrogen content of the fruit. This was directly correlated with susceptibility to scab on the tree and to rotting in store. The rate of radial advance of the apple-rotting fungus *Cytosporina ludibunda* was fifteen times greater on apples from the plot treated with nitrogen and potash than on those from the plot treated with potash alone.

Concerning infections of the leaves, it has been shown by Dr Katharine Johnstone that individual trees in pot-culture experiments demonstrate clear-cut relationships between nutritional status and scab susceptibility. Trees deficient in nitrogen show fewer infections and a much diminished persistence of individual lesions by comparison with those fully fed: those deficient in potash, on the other hand, exhibit enhanced susceptibility and increased persistence of lesions. Miss Johnstone's experiments on the toxicity of expressed leaf liquids, following earlier work by Dr Wiltshire, further indicated that the liquid expressed from apple leaves in the nitrogen-deficient series was more toxic to scab spores than that from the leaves of the trees receiving the remaining manurial treatments.

From results reported by Prof. Wallace on *Pseudopeziza* infection of black currants in relation to manurial treatments, a different picture emerges. Here, potash deficiency increases resistance to the disease while lack of nitrogen or of phosphate decreases it. This differentiation of effect on the Leaf Spot attack was of such magnitude that the anticipated adverse effect of omitting potash was partially outweighed by the unexpected beneficial action of this treatment in reducing the disease.

In controlling plant diseases, any practice whereby spraying might be reduced or eliminated is always worth attention, and this lends special interest to some of the interactions of manurial treatments and fungus infections. In Chocolate Spot of beans it is seen that resistance may be increased by correcting phosphate and potash deficiencies but that the occurrence of infection cannot be obviated by such treatment.

In other examples it is possible to attain something nearly approaching immunity but only at the expense of the general health of the host. In apples, Scab resistance is increased by lowering the nitrogen content of the leaves and fruit, and to a certain extent the benefits of spray applications can be supplemented by manurial treatments. But any attempt to reduce the nitrogen level to a point where spraying could be dispensed with would result in the production of a starved, stunted tree with fruits that were indeed uninfected but meagre morsels whose brilliance of complexion fails to compensate for a lamentable lack of flesh.

Again I have instanced black currant Leaf Spot where the attack can largely be averted by subjecting the bush to potash starvation. This too is dangerously close to the practice of curing the disease by killing the patient.

There are a number of records of the application, for the control of specific fungus diseases, of materials taken up by the plant, whose role in nutrition is still undetermined. G. T. Spinks showed in 1913 that the addition of lithium salts to a water-culture medium was remarkably effective in preventing Mildew on wheat grown in pot cultures. Dr N. L. Kent corroborated these observations in 1941 and demonstrated that watering with lithium chloride or nitrate at suitable concentrations reduced the amount of Leaf Spot disease in celery and at the same time increased the weight of the plants. This treatment also reduced the susceptibility of wheat seedlings to Brown Rust.

An analogous method of investigation is by the injection technique perfected at East Malling by Dr Roach. He has published an interesting example of the use of sodium thiosulphate for direct shoot tip injection of apple trees, with a resulting increase in resistance to Apple Mildew.

Such examples point the way to disease control by nutritional means, but at present it appears that nutritional treatments are likely to be useful adjuncts to other control measures, rather than substitutes.

A neighbouring arena into which one ventures with trepidation is that of the relation between fungus diseases and the source of manure, i.e. whether organic or inorganic. To hear some of the more fervent reciters of the compostolic creed, one would imagine that the research stations harboured a subversive organization of soil saboteurs, poisoners of the good earth, fosterers of pests and diseases, destroyers of fertility in plant, man and beast, whose final aim was a sterile world, thickly encrusted with sulphate of ammonia. But in the realms of fact there are no compost haters. The crux of the problem is, that supplies of organic manures are insufficient and have to be eked out. Even in a garden, working on a spade and wheelbarrow scale, it is rare to find that sufficient compost can be made and distributed annually to maintain a high level of soil fertility. And if we consider the problem of a farm with, say, fifty acres of arable land, the collecting, making, hauling and spreading of the tonnage of compost required for this acreage would require an expenditure of time, labour, water and transport far beyond the capacity of the equipment available. The farmer has every encouragement from the soil scientist to use organic manures up to the economic limit, but there is almost inevitably a deficit to be met between the nutrients removed by a crop and those returned in organic manures. These deficits can be economically made up only by the use of mineral fertilizers, and it is the work of the soil chemist to determine how this may best be done. It seems particularly hard that in these times the soil chemist should be accused of promoting an excessive use of 'artificials', when he has in the past five years worked in an environment of rationing and limitation of supplies and, more often than not, has been concerned to find out not how much, but how little inorganic manure, it was practicable to use.

All this may possibly be termed a diversion, but there is one point on which the mycologist feels he must take issue with those whom Prof. Salisbury has termed 'muck-minded'. Some of them have been known to state (for example) that potatoes grown with (and, by inference, because of) compost remain free from Blight, whereas those grown with inorganic manures succumb to the disease. Such statements might not seem worth controverting, but they are made so persistently and have apparently gained credence in such exalted quarters that there seems nothing for it but to carry out a series of *ad hoc* experiments to show where the truth in these matters is to be found.

An experiment recently described by Dr Croxall is of interest in this connexion. He grew onions in a series of plots given a selection of manurial treatments including farmyard manure, sludge with town refuse compost, a complete inorganic dressing, compost plus inorganic nitrogen, etc. One would expect that an onion bulb with its prolonged and intimate contact with the surface layers of the soil would have an excellent chance of contracting any fungus infection supposedly promoted by the use of inorganic manures. However, when Dr Croxall recorded the fungal rots in the stored onions he found that the percentages of rots from the onions grown with the treatments mentioned showed no significant difference due to manuring.

The study of the materials used for the control or prevention of fungus growth is one in which little progress can be made without the closest co-operation between the mycologist and the chemist. At first sight it might appear that such studies added little to our knowledge of the biological processes of the fungi concerned. However, these investigations have provided us with a completely new chapter of mycological knowledge concerning the exudates produced on the germination of fungus spores. Outstanding contributions to this elucidation of the mechanism of interaction between spore and fungicide have come from the partnership of McCallan and Wilcoxon at the Boyce Thompson Institute. The conception that spore exudates exist and play a major part in bringing copper into solution has greatly widened the choice of water-insoluble copper materials which may thus be made available as fungicides. A systematic study of this field by Dr Hubert Martin and his co-workers has led to the development of a wide series of commercial copper sprays whose suitability for amateur use has been of particular value in war-time. It is not too much to say that the intensive work on new fungicides in the past decade is revolutionizing the realm of spray materials.

I have touched only on the copper sprays and to go further in this direction would take me too far from my course. Where, however, the crop to be sprayed is of special value as a source of vitamin C (the fruit of black currants for example), the presence of copper spray residues antagonistic to this vitamin would obviously be undesirable. Hence the present interest in the development of non-metallic sprays such as the thiocarbamates, the aim being the derivation of a spray which combines satisfactory field performance with the absence of any residue adversely affecting the nutritional and processing value of the crop.

There are obvious advantages to be gained by the association of a mycologist with an entomologist, for example in the planning of spraying programmes. In reading accounts of tests of fungicides in American orchards it is useful to be reminded of the overriding claims of codling moth control in that country. Papers have been written from which the unwary reader would assume that the fungicides used were diluted with water in the accepted fashion, but on further inquiry it is discovered that the fungicides were in fact added to a suspension of lead arsenate, the use of arsenicals being such a matter of course in the American programme that the writer of the paper thought it not worth mentioning. More particularly, the results of American tests with various sulphur suspensions are subject to the reservation that these relatively weak fungicides are added to each of a long succession of arsenical applications which reinforce both the tenacity and the fungicidal effect of the sulphur deposits.

In this country, one of the weightiest reasons for the popularity of lime sulphur in the apple-spraying programme is the fact that this spray has a certain value in the control of Red Spider. The natural reluctance of the grower to apply two sprays when one will do has again led to the development of combined insecticide-fungicide applications and incidentally stimulated the study of wetting agents which were not, like soap, incompatible with lime sulphur. The success of the orchard entomologists in shifting much of their insect control programme to the relatively unhurried days of winter has led to investigations into the possibility of dealing also with apple scab at that season. Wide use is being made of di-nitro-cresol in winter washing and it has been shown by Keitt in Wisconsin that di-nitro-cresol spraying of orchard soil on which overwintered leaves are lying (the so-called 'floor spraying') prevents the maturation of apple scab ascospores in the treated leaves and thus renders easier the control of scab in that orchard in the ensuing season. While the problem is complicated in this country by the existence of unassailable shoot and bud infections on certain apple varieties, there are many plantations, for example those of Bramley's Seedling, in which scab infection in spring can arise only from overwintered leaves. Co-operation with the entomologist in trials employing di-nitro-cresol in such plantations might well give valuable results.

Other types of dual-purpose sprays are beginning to come into use. Manganese deficiency in apples is controllable by the addition of manganese sulphate to the routine lime sulphur applications. Materials for preventing pre-harvest drop of fruits (e.g. α-naphthalene acetic acid) might similarly be combined with late fungicidal applications designed to check storage rots.

The results of the association of mycologists with workers in other fields of agricultural science are not limited to securing a fuller understanding and a more rapid solution of the problems dealt with by joint study. The stimulus for the initiation of many classic mycological studies has come from the importance to agriculture of disease-producing fungi. It is highly unlikely that mycology would be enriched by so much detailed knowledge of *Puccinia graminis*, *Phytophthora infestans*, *Venturia inaequalis* and *Botrytis*

cinerea were they not pathogens of valuable agricultural crops. Further, the mycologist, working, for example, with a plant physiologist, has his interest aroused in the physiological aspects of the fungus under study and learns to adopt for his purposes the techniques developed by his colleagues. All the resulting information gained trickles back into and swells the main stream of mycological knowledge. If it is in order, I should like to quote this sentence from the Society's unpublished report on systematic mycology: 'The pathologist carries out experiments on the biology and pathogenicity of his fungus, during the course of which a body of valuable and essential data on the effect of host and other experimental conditions is obtained, and this is of the utmost reciprocal value to the systematist for determining new standards in classification and nomenclature.'

The point I have attempted to make is that the association of mycology with agricultural science has enlarged the content of pure mycology. This fruitful association is paralleled by the links between mycology and forestry, a subject needing no further treatment here since it was admirably covered by Mr Cartwright's Presidential Address in 1937.

Industrial and medical mycology

These agricultural and silvicultural sections of our subject I might group under the title of rural mycology. There exists also an urban mycology: mycology in its industrial and medical aspects. Considering only the main headings, there are the fungi attacking man and animals; those causing food spoilage and deterioration of textiles and paints. There are fungi used as sources of protein for human consumption, such as *Torulopsis utilis*, soon to be in large-scale production in Jamaica. Then the yeasts, no longer used only by brewers and bakers (I may add cider makers), but of fundamental importance in maintaining the production of industrial alcohol which is destined to play a more and more important part as increasing inroads are made on the world's petroleum supplies.

The large-scale culture of fungi for the utilization of their metabolic products is one of the aspects of industrial mycology in which developments have been most spectacular. Glycerol, acetone, citric and gluconic acids, ergosterol, invertase, quinones and mould pigments are but random examples of the products of the investigations (notably those of Dr Raistrick and his collaborators) in the biochemistry of moulds. And finally, we have the range of therapeutic derivatives on one of which, penicillin, a new industry has been based. Among the list of recipients of the Society's recent Report on systematic mycology were the Research Associations of the cotton, woollen, flour milling, printing, cocoa and chocolate, distilling and brewing industries, the Food Manufacturers' Federation, the Building Research Station and the Pharmaceutical Society. This list suggests a few of the directions available for the expansion of our interests.

In all these fields there are, as in rural mycology, workers who have accumulated knowledge of their fungi and have broadened this knowledge through contact with their colleagues in other sciences. It is reasonable to assume that urban mycology has much to contribute to our Society,

but I would suggest that we have room for a more widespread appreciation of the opportunities open in this field.

The development of contacts between academic mycology and its applied side is bound to be influenced by the place allotted to mycology in University curricula. The whole field of the methods of training of entomologists and plant pathologists is being actively studied by the Plant Pests Committee of the Association of Applied Biologists, whose report will be of great value in this connexion. A recent draft report on university research made by the Association of University Teachers also touches on this topic. This suggested the formation of Departments of Mycology, without, however, defining the status of the proposed departments. There is here, I feel, a possible danger to be guarded against in that the system existing in some American universities may creep in, whereby an undergraduate can specialize in mycology without having first laid any foundation of general biology. On the other hand, the present position of mycology in our under-staffed university departments of botany cannot be considered satisfactory. Some of us have been fortunate, but many students on looking back on their botanical training must be left with the impression that the fungi come in as a footnote to the phylogenetic morphology of the ferns. There is obvious room for mycologists who also know something of plant physiology, or of chemistry or of horticulture, but I know of few mycologists who have been able to find any use for the knowledge they have perforce accumulated of the Horsetails, the Mosses and the Seaweeds.

The links between botany and mycology in the British universities do, however, provide sufficient common ground for the mycologists to enter into the problems of plant physiologists, geneticists and other workers in agricultural sciences. There is, however, no system of training yet worked out suitable for the industrial mycologist, whose progress has been in directions where a botanical training provides little guide.

Individual members have already done much to establish links between our Society and these newer developments of mycology. There could hardly be a more comprehensive survey of the applications of fungi in industry and medicine than Dr Ramsbottom's address on the uses of fungi made to Section K of the British Association in 1936, supplemented by his 1944 lectures at the Royal Institution. Dr Wiltshire has just published a pioneer bibliography of medical mycology, and Mr George Smith's text-book of industrial mycology is indispensable. But, taking the Society's publications as a criterion, there are in the 3280 pages of the last ten volumes of our *Transactions* only forty-four which could be considered to treat of species selected for their industrial or medical interest.

The publication of work on the fungal therapeutants has now been for some years subjected to a war-time black-out. But it is at least to be regretted that none of the results of the pre-war investigations of the bacteriostatic action of fungi found their way into our *Transactions*. Many mycologists must find it humiliating to confess that their knowledge of penicillin has been gleaned almost entirely from the popular press. It is, of course, not a question of blaming individual workers for not beseeching the Society to hear them: the fault is in ourselves as a Society that our

scientific curiosity was not strong enough to overcome the difficulties of obtaining informed opinion on this section of our subject.

Now it would seem that chinks in the black-out are appearing, and some of the mycological details of penicillin production are being uncovered. A letter to *Nature* in August referred to penicillin-like antibiotics from a range of mould species. An article in the American Chemical Society's *Chemical and Engineering News* for 25 April of this year also records that penicillin is not exclusively a product of *P. notatum* but may also be formed by *P. chrysogenum*. Further, this article gives in reasonable detail the three most important production techniques and the methods for biological assay.

One unfortunate result of the apparent lack of interest of this Society in industrial and medical mycology is that the Society is not in any way considered when Government Committees are set up to deal with these matters—the Penicillin Committee for example. Again, when a Committee was first set up here to investigate fungal spoilage of military stores in the Western Pacific, this Society apparently remained as unknown to the Committee as the Committee did to this Society.

While much must still remain hidden, we can now begin to look back and discern outlines of the dramatic developments, the massive contribution, that mycology has made in the past five years. But while mycology has come to the fore, our Society, as a society, has not moved from the background. The war record of British mycology is exhilarating: that of the British Mycological Society is—well—blameless. Mycology has blazed up but we have not been illuminated.

It is not necessary to labour the point that it is in every way in the Society's interest to combat this attitude of apathy towards urban mycology. Widening our field of membership would confer obvious advantages on the Society. The Associate Member scheme is one valuable step in this direction: the other major source of recruits is in the rapidly expanding sphere of industrial mycology.

Relations with other societies

This, however, raises another problem which becomes more and more insistent yearly. There already exists a competition, not perhaps realized but none the less real, for the subscriptions of new entrants into the biological professions. With the probable post-war pullulation of scientific societies, this competition will become a matter of serious concern alike to old and to new biological associations. A young man or woman in his first post cannot be expected to contribute guineas to half a dozen scientific societies simultaneously. The resulting dissipation of effort has obvious disadvantages.

This is, of course, no new contention. It has been brought forward by many who are concerned over the future of our publishing societies, notably by Dr Martin in his recent presidential address to the Association of Applied Biologists. Again, as an example of the type of scheme which has been frequently suggested, I would call attention to Dr Darlington's

proposals. Dr Darlington envisaged a series of steps towards a system of federation, one of the first of these steps being an annual meeting of secretaries or delegates of biological societies to make arrangements for matters of joint interest in meetings, publications and general policy. In such a matter there is obviously the necessity for a lead to be given by an organization at a higher level than that of the individual societies. The name which comes first to one's mind is the Royal Society's National Committee on Biology. I do not know in what state of preservation this body is to be found, but as it has been functionless for some twenty-one years, there are grounds for assuming it to be now a vestigial structure. More, I trust, can be hoped of the newly proposed Biological Council sponsored by the Biochemical Society.

On such a central organization one might envisage some co-ordination of dates of meetings and of subjects between, for example, the A.A.B., the Microbiological Panel of the Society of Chemical Industry, the Society for Microbiology and our own Society. Members of any one of these societies should be welcomed at meetings of others in the group, and I hope that our Society, the senior of the four mentioned, would be the first in acting as host to the others. A further step, which might prove practicable in the near future, would be to extend our scheme of Associate Membership to include any full member of these societies without further qualification. This would make for larger and more varied audiences at our meetings, extending the links between systematic and applied mycology and making contacts valuable to our Society. There are people who have been using fungi simply as reagents, and some of these, whose concern hitherto has been only with what a fungus does, may be stimulated to find out what it is. As their interest develops they will wish to have our publications and to take up full membership.

Developments along these lines would help to overcome the immediate financial difficulties both of the societies and of their members, actual and potential. Further, as many new members would come in by introduction so to speak, from one society to another, it should do much to dispel any atmosphere of rivalry or disunity among those with interests in common.

I know that I have in many respects departed from the conventions of a Presidential Address, and I am conscious of having generalized on subjects of which I have no detailed knowledge. While the means are open to criticism, the end is plain—to recall attention to the first rule of our Society: that 'its object shall be the study of mycology in all its branches'.

STACHYBOTRYS AND *MEMNONIELLA*

By G. R. BISBY, *Imperial Mycological Institute, Kew*

The publication of my paper (1943) on *Stachybotrys* has been followed by the receipt of numerous cultures and collections. *S. atra* Corda proves to be common also in warmer areas and in the south temperate, and most of the cultures studied were like the 'standard' English culture I described in some detail. Singer's (1944) opinion, 'The theory of the prevalence of cosmopolitism in fungi ought to be abandoned altogether', may apply to boleti and agarics, of which he was writing, but does not apply to many moulds. It is true that there is variation in *S. atra*, but I have detected no evidence of 'geographic variation'.

Prof. G. W. Martin sent a specimen of *S. atra* from Iowa with the note that each of the phialides had a septum at the base. I could see quite clearly that he was right, and I doubtless should have been able to demonstrate septa previously, for I expected their presence. The phialides of *S. atra* seem to differ from the usual phialides only in their shape.

It happened that a paper by Hansford (1943), with three new species of *Stachybotrys*, appeared at about the same time as mine. I have now seen the type collections of his species. *S. kampalensis* Hansf., with conidia 10–14 × 6–8 μ, would formerly have seemed distinct from *S. atra*; but my interpretation of *S. atra* includes conidia of that size. *S. nephrospora* Hansf. is similar to *S. atra* except in having somewhat curved conidia. From the manner of formation of conidia of *S. atra* in heads, one might expect some curvature; but the fact remains that the conidia are usually symmetrical. Perhaps *S. nephrospora* will prove to be a distinct variety of *S. atra*. Cultures and further collections of these two species found in Uganda are awaited.

S. Theobromae Hansf. is an interesting discovery. The conidia are described as 20–28 × 15–18 μ on phialides 21–28 × 7–10 μ. My mounts showed that the phialides start to form in the manner usual with *Stachybotrys*, i.e. a terminal phialide is formed; another starts just below the septum which delimits the first, and is in turn provided with a septum; then a third phialide commonly develops. As Hansford states, no more than three phialides are evident. In the dried material mounted in water I did not see a spore longer than about 24 μ, and many are 17–20 × 15–17 μ. This collection is the second of a large-spored *Stachybotrys*, the first being *S. crassa* Marchal described fifty years ago in Belgium with 5–7 phialides 17–21 × 10–12·5 μ, spores globose, 16–18 μ. Marchal attempted cultures, but did not obtain conidia. It seems possible that, if this large-spored species shows variability comparable to that found in two other species of *Stachybotrys*, *S. crassa* and *S. Theobromae* may prove to be the same species; while we suspend judgement, we can tentatively add one species to the two I recognized previously.

I have seen only one more collection, found on germinating rice seed

in Uganda, of *S. subsimplex* Cooke. The description and figures of *S. Voglinii* Cif. (1922, p. 48) suggest *S. subsimplex*. I suspect that some of the recent reports of *S. papyrogena* (Sacc.) Sacc. refer to *S. subsimplex*, but I do not yet know what *S. papyrogena* is.

Dr Machacek, who supplied the 'pink *Stachybotrys*' I described briefly, writes that he has seen a few more similar cultures from soil in Manitoba. It may, therefore, prove to be a good new genus and species, but I have seen no more collections or cultures.

Cultures and data from Dr Lilian Fraser of Sydney and R. M. Brien of Auckland show that *Memnoniella echinata* (Riv.) Galloway is a common fungus, especially on old cloth in certain warmer areas. It regularly produces persistent chains of conidia without slime. The cultures agree with Galloway's description and culture, and the fungus is distinct from *Stachybotrys subsimplex*.

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A NOTE ON MEDLAR CLUSTER-CUP RUST (*GYMNOSPORANGIUM CONFUSUM* PLOWR.) IN KENT IN 1943 AND 1944

By M. H. MOORE, *East Malling Research Station*

(With Plate I)

Plowright's description (1889) of the aecidial stage of this rust was based upon infections artificially induced on *Crataegus oxyacantha*, *Mespilus germanica*, and *Pyrus* (*Cydonia*) *vulgaris*, with teleutospores from the perennial mycelium in *Juniperus Sabina*. Fischer (1904) also described it; he produced aecidia on the same three hosts and on *Crataegus monogyna* and, 'more seldom', on *Pyrus communis*, the teleutospore hosts being *Juniperus Sabina* and *J. virginiana*.

Its natural occurrence on medlar evidently is not common, for only two references to it can be found in the literature: (i) by Fischer (1904) in Berne in 1885 and (ii) by Wormald (1931), who reported that 'Medlar Cluster-Cup Rust (*Gymnosporangium confusum*) was present on a few leaves of a medlar tree on this Station, and on a single quince leaf', which thus appears to be the only record for Britain.

A severe attack was seen in July 1943, on the leaves and fruits of a medlar tree in an East Malling garden. The tree, a standard, was about 10 ft. high and 12–15 ft. in diameter, and near it to the east were two bushes, carpeting the ground, of a small-leaved variety of *Juniperus Sabina*. The nearer one was about 12 ft. from the medlar, the east side of which was much more severely affected than the west, and on this savin was found a shoot with a fusiform hypertrophy characteristic of infection on juniper. Though sterile when examined, it may have borne teleutosori earlier. It has been established that the medlar was from a batch of young nursery trees on one of which Wormald first observed the disease. They were at that time on a plot just outside this garden where the two savins were already growing. The rust has probably been present on this tree many times since, passing unnoticed until 1943.

Symptoms. The scattered leaf-spots, as seen on the upper surface, were roughly circular, slightly convex, and about 0·5 cm. in diameter. Most of them, brown in the centre, were surrounded by a conspicuous yellow, orange-streaked halo (Pl. I, fig. 1), and many bore spermagonia. The yellowish to pale brown, curved, cylindrical aecidia, up to 4 mm. long, arose from slightly thickened corresponding areas on the lower surface; they were occasionally found also on the upper surface. There were many affected fruits among the heavy crop and they bore similar aecidia on swollen areas, mostly on the fruit itself but sometimes on the calyx.

By October affected fruits had all dropped, leaving a good crop of healthy ones. There was no sign of leaf-drop in spite of the numerous

infections. The lesions had not developed since July and even severely affected leaves were turgid; the aecidia had dried up, leaving little trace. There was much healthy new foliage, and the disease had evidently not progressed after teleutospore production ceased.

In 1944 infection had already occurred by early June, but it was slight compared with that in 1943. Aecidia were present, but mostly not mature, and they were shorter (*circa* 2 mm.) than those of 1943. On incubation for a day or so in moist air they matured and split throughout their length, releasing clouds of spores. The savins were searched for teleutosori, and several shoots were found with fusiform hypertrophies about 5 cm. long. Parts of the bark had split and curled back revealing pale, cortical swellings up to 4 × 3 mm., but no teleutosori were seen on the dry field specimens. Incubation in moist air, however, induced a few pale, gelatinous spore masses to arise beneath the flaps of bark, and revived a few brown teleutosori about 5 mm. long (Pl. I, fig. 2).

The fungus. Spore measurements conformed in general to those of Plowright and of Fischer, but showed slight differences.

(i) *Thick-walled teleutospores*, 38–50 × 20–26 μ, av. 44 × 24 μ (Plowright: 40–50 × 20–25 μ; Fischer: 35 × 25 μ), brown, broadly oval to fusiform, two-celled, with long pedicels.

(ii) *Thin-walled teleutospores*, 40–50 × 19–24 μ, av. 45 × 20 μ, with orange, granular contents.

(iii) *Basidiospores*, 4–6 × 2–3 μ, oval, hyaline.

(iv) *Aecidiospores*, 22–26 μ, av. 24 μ (Plowright: 15–20 μ; Fischer: 21–24 μ), pale brown, globose, minutely verrucose.

Grove (1913) gives: (i) 30–50 × 20–25 μ, (iv) 21–24 μ.

Plowright remarked of *Gymnosporangium confusum* that 'this species has hitherto been confounded with *G. Sabinae*, which it resembles in many points'. It has the same teleutospore host (*Juniperus Sabina*), but the sole aecidial host of *Gymnosporangium Sabinae* is stated by Fischer to be *Pyrus communis*, a 'difficult' host for *Gymnosporangium confusum*. Other differences (from Grove, 1913) are that in *G. Sabinae* the aecidiospores are larger (28–30 μ), the aecidia are flask-shaped, not cylindrical, the teleutosori are longer (8–10 mm.), and the teleutospores, while about the same length, are slightly broader (40–50 × 25–30 μ) than those of *G. confusum*. According to Fischer, *G. confusum* is biologically closely akin to *G. clavariaeforme*, the aecidial hosts of which are *Crataegus oxyacantha*, *C. monogyna*, and *Pyrus communis*, with *Juniperus communis* as the teleutospore host. The aecidia of this species resemble those of *Gymnosporangium confusum*, but the aecidiospores, like those of *G. Sabinae*, are larger (28–30 μ).

Weather relations. The following data concerning the distribution of wind and rainfall in May, when medlar leaves have unfolded, are relevant to the severity of infection in 1943 and its comparative lightness in 1944. As the medlar was to the west of the savins, the basidiospores, after being forcibly abjected from the basidium (Coons, 1912; Buller, 1924), would need easterly winds in May to carry them up to the medlar. May 1943, with easterly winds on eleven days, and a total rainfall at East Malling of 2·82 in. (1·01 in. on 1st), was alternately dry and wet, with mostly dry

Fig. 1.

Fig. 2.

easterly winds during the first and third weeks, and mostly wet westerly ones during the second (1·29 in.) and fourth (0·47 in.). The basidiospores, produced under the stimulus of moist conditions, could thus have been continually carried up to the medlar shortly before a rainy spell during at least two periods. May 1944 had easterly winds on twelve days, but the month was very dry with a total rainfall of only 0·48 in., 0·30 in. of this on the 16th.

Control. The removal of the savin from the locality would be an effective means of controlling this rust, or the cutting-out of hypertrophied shoots before they produce teleutospores could be attempted, but in an ornamental garden or a nursery this is not always desirable, and spraying the medlar in spring with Bordeaux mixture (4–6–100) or some other suitable copper preparation would be worthy of trial. Duggar (1909) regarded the spraying of the aecidial host with standard Bordeaux mixture 'at about the time of ripening of the teleutospores' as of some value; Grove (1913), however, stated that 'it is useless to spray the aecidial host'.

Summary

A severe aecidial attack in 1943 and a slight attack in 1944 of the uncommon Cluster-Cup Rust, *Gymnosporangium confusum* Plowr., on *Mespilus germanica* in a Kent garden are described. Two bushes of a variety of the teleutospore host, *Juniperus Sabina*, were growing nearby.

The writer is indebted to Mr R. V. Harris for his helpful criticism in the preparation of this note, to Mr W. C. Moore for a summary of the literature, to Dr H. Wormald for his helpful interest throughout, and to Mr D. Akenhead for a translation.

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EXPLANATION OF PLATE I

Fig. 1. Medlar Cluster-Cup Rust on leaves and fruit (× approx. $\frac{3}{4}$).
Fig. 2. Hypertrophied branch of *Juniperus Sabina* with teleutospore stage of *Gymnosporangium confusum* Plowr. (nat. size). Note revived teleutosorus protruding on left.

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ON THE SPECIALIZATION OF *BREMIA LACTUCAE* ON COMPOSITAE

By LEE LING and M. C. TAI, *Chengtu, China*

(With Four Text-figures)

Introduction

The genus *Bremia* was established by Regel in 1843 for the single species *B. Lactucae*, which has remained the best-known species of the genus and has been reported from widely separated regions. In addition to *Lactuca*, members of the following genera of Compositae have been recorded as host plants for *Bremia*: *Carduus*, *Carthamus*, *Centaurea*, *Cichorium*, *Cirsium*, *Conyza*, *Crepis*, *Cynara*, *Gaillardia*, *Gnaphalium*, *Hieracium*, *Krigia*, *Lappa* (*Arctium*), *Lapsana* (*Lampsana*), *Leontodon*, *Picris*, *Prenanthes*, *Senecio*, *Sonchus*, *Taraxacum*, *Tragopogon*. Schweizer (1919) concluded, from the results of his observations and experiments, that *Bremia Lactucae* includes a number of biologic forms which are specialized to distinct hosts and may be separated to some extent on biometrical data. Sydow (1923, 1938), following Schweizer, separated three of these forms as distinct species, namely, *B. Tulasnei* (Hoffm.) Syd. (from *Senecio*), *B. Centaureae* Syd. (from *Centaurea*) and *B. Lampsanae* Syd. (from *Lapsana*). Sawada (1919) named five species from Formosa, namely, *B. elliptica* Saw. (from *Lactuca laciniata* Makino = *L. indica* L. and *L. formosana* Maxim.), *B. microspora* Saw. (from *Lactuca debilis* Mass.), *B. sonchicola* (Schlecht.) Saw. (from *Sonchus oleraceus* L.), *B. ovata* Saw. (from *Crepis japonicus* Benth.), and *B. Saussureae* Saw. (from *Hemistepta carthamoides* O. Kuntze = *Saussurea affinis* Spreng.). Ito (1938) listed a few additional hosts for *B. elliptica*, *B. microspora* and *B. sonchicola*. Itọ and Tokunaga (1935) had already described two new species from Japan, *Bremia Taraxaci* and *B. Picridis*. Milovtzova (1937), working in the Ukraine, held the mildew on *Carthamus tinctorius* L. to be a new form, *Bremia Lactucae* Regel f. *Carthami* Milovtzova. Jagger and Chandler (1933) and Schultze and Röder (1938) demonstrated the existence within *Bremia Lactucae* of a number of physiologic races by showing that the various forms differed in their pathogenicity towards varieties of the cultivated lettuce.

Between 1942 and 1944, *Bremia* has been collected in the vicinity of Chengtu, China on the following seven host plants: *Lactuca sativa* (leaf type), *L. indica*, *L. chinensis* Makino, *Crepis japonicus*, *Sonchus oleraceus*, *Taraxacum mongolicum* Hand.-Mzt., and *Saussurea affinis*. Except for the fungus from *Lactuca chinensis*, these collections of *Bremia* had already been recorded and assigned to six distinct species. As it was possible to obtain all these forms in abundance, there was an excellent opportunity for a comparative study on which the taxonomic relationships of the forms could be ascertained.

Comparative morphology

Details of the morphology of *Bremia* collected from the seven hosts are given in Table 1; Figs. 1 and 2 illustrate the results of five hundred measurements of the lengths and widths of the sporangia of the seven collections. All observations were taken from fresh material mounted in lacto-phenol or, rarely, in distilled water. A study of Table 1 and of the corresponding text-figures shows that the collections of *Bremia* from the seven hosts can be arranged in three groups. The fungus from *Saussurea* is distinguished by its large sporangia, and the measurements from this material overlap very little with those from the other gatherings. The fungi from *Lactuca chinensis* and *Crepis japonicus* have small sporangia, and the rest form a third group with sporangia of medium sizes.

The shape of the sporangium, taken by itself, is not a reliable guide for the separation of species. In a single gathering, sporangia ranging in shape from subglobose to elliptical may be found (Fig. 3). Sawada applied the specific epithet *ovata* to the *Bremia* on *Crepis japonicus*, but ovate sporangia may be found in greater or less numbers in most gatherings. The length/width index shows that the sporangia of the fungus from *Crepis japonicus* are more elongated than sporangia taken from other host plants, but the difference is not great enough to make it possible to separate the various forms by microscopic examination.

The *Bremia* from *Crepis japonicus* has very long sporangiophores, ranging from 850 to 1050 μ in length; this character agrees with the original description of *Bremia ovata* from the same host. The other characters of the sporangiophores, such as the method of branching, and the proportion between the lengths of the whole sporangiophore and of the unbranched portion, characters which were emphasized by Sawada (1919), are too variable to be used for taxonomic purposes. In their morphology, the fungi from *Lactuca sativa* and *L. indica* agree more closely with one another than with those from the other hosts.

Inoculation experiments

Between December 1942 and February 1944, many cross inoculations were made. The inocula were obtained, in part from naturally infected hosts growing in the open, and in part from artificially infected hosts in the laboratory. The inoculations were made by spraying healthy host plants with suspensions of sporangia in water. Satisfactory results were obtained by using water rich in minerals, and especially in salts of calcium and magnesium, taken from a well; it had already been found that the sporangia germinated better in this well water than in rain water, river water or distilled water. The poorest germinations were obtained in distilled water, which gave germination percentages of 23 % after 128 hours and of 36·7 % after 176 hours; the corresponding figures for well water, river water and rain water were: after 128 hours, 62·8, 45·4 and 34·2 %; after 176 hours, 63·1, 60·7 and 51·6 %.

Table 1. *Morphology of* Bremia *on seven species of Compositae*

Host	Morphology of sporangiophores: Sporangiophore growth	Times of branching	Length in μ	Width in μ	No. of sterigmata	Morphology of sporangia: Average shape	Length* in μ: Range	Length* in μ: Mean	Width* in μ: Range	Width* in μ: Mean	Length/width
Saussurea affinis	Amphigenous, dense	4–7	206–650	7·6–11·4	3–6	Broadly elliptic	22·9–37·2	30·37 ± 1·120	20·0–32·9	27·77 ± 0·908	1·09
Lactuca sativa	Mostly hypophyllous, dense	3–6	275–420	11·4–15·2	3–5	Subglobose	10·0–24·3	17·61 ± 1·073	10·0–22·9	16·26 ± 0·807	1·08
L. indica	Mostly hypophyllous, dense	4–6	425–610	7·6–14·3	4–7	Subglobose	11·4–24·3	17·50 ± 0·982	11·4–22·9	16·40 ± 1·028	1·06
L. chinensis	Hypophyllous, sparse	4–6	310–510	9·5–13·4	3–5	Subglobose	10·0–21·5	15·32 ± 0·897	8·6–20·0	14·05 ± 0·851	1·09
Crepis japonicus	Hypophyllous, sparse	5–8	850–1050	7·6–11·4	4–7	Ovate to elliptic	10·0–21·5	15·63 ± 0·971	7·2–19·2	11·89 ± 0·777	1·31
Taraxacum mongolicum	Hypophyllous, sparse	4–6	428–545	9·5–13·4	3–6	Broadly elliptic	12·9–24·3	18·54 ± 0·886	11·4–21·5	16·49 ± 0·882	1·12
Sonchus oleraceus	Hypophyllous, dense	3–6	332–534	11·4–13·4	3–6	Broadly elliptic	12·9–24·3	18·54 ± 0·943	8·6–21·5	16·12 ± 1·066	1·14

* Based upon 500 measurements

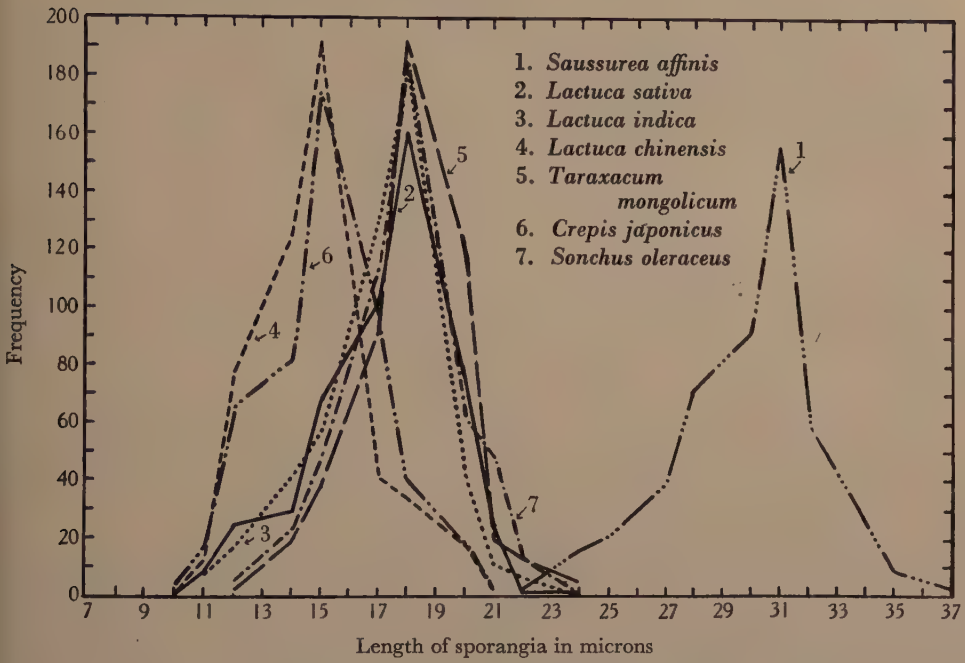

Fig. 1. The distribution in length of 500 sporangia of *Bremia* on seven hosts.

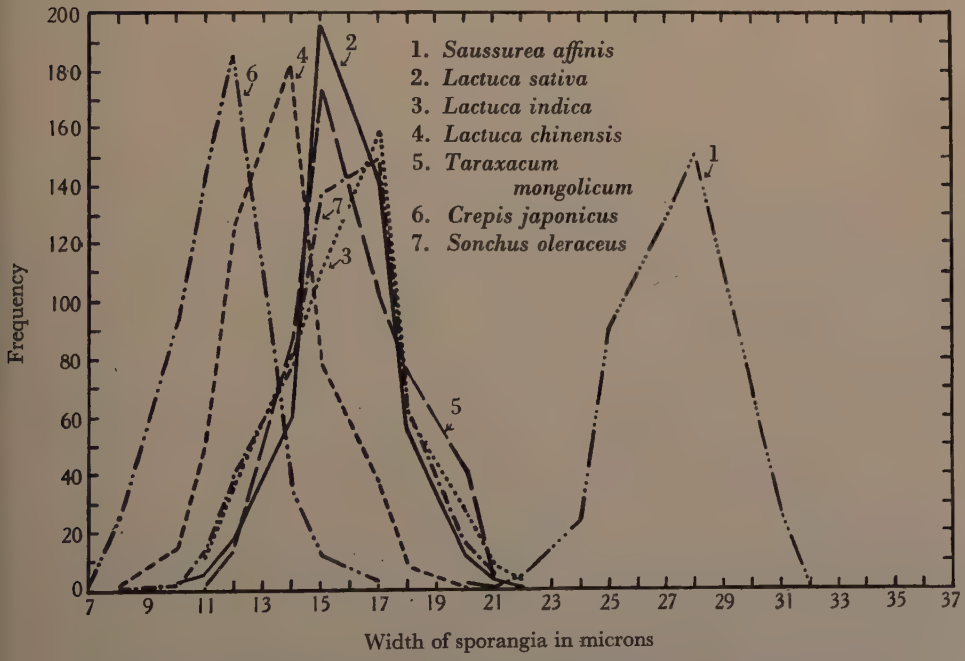

Fig. 2. The distribution in width of 500 sporangia of *Bremia* on seven hosts.

After the host plants had been inoculated they were kept in a moist chamber for two to three days; detached leaves were also inoculated to give a check on the experiments with growing plants. If the host was susceptible to the fungus, sporangiophores appeared in from nine to twelve days after inoculation. The results of the experiments are summarized in

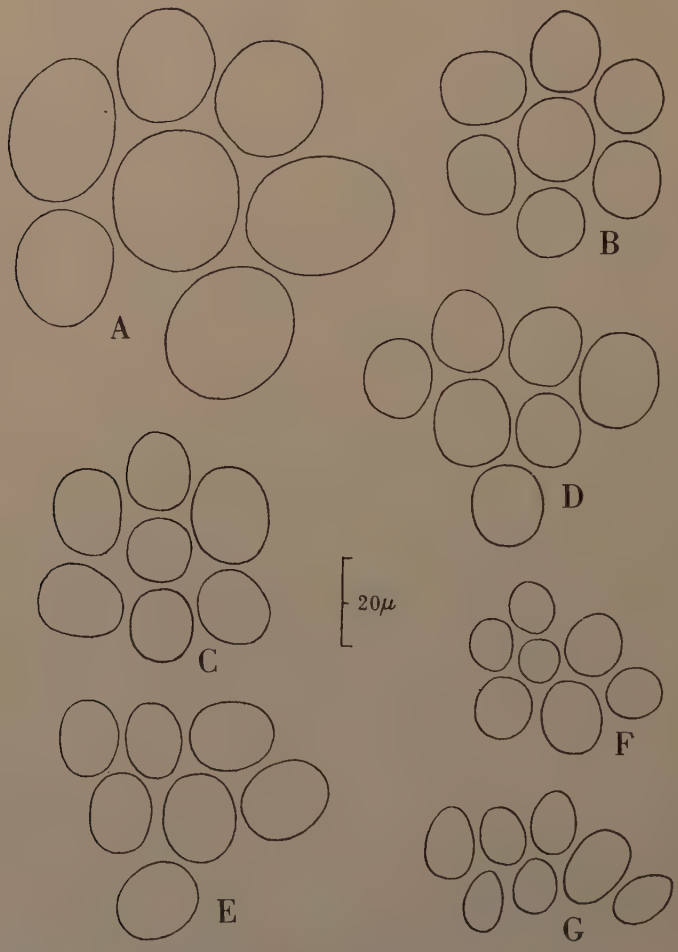

Fig. 3. Sporangia of *Bremia* on seven hosts. A, *Saussurea affinis*. B, *Lactuca sativa*. C, *Lactuca indica*. D, *Sonchus oleraceus*. E, *Taraxacum mongolicum*. F, *Lactuca chinensis*. G, *Crepis japonicus*.

Table 2. They show that cross-inoculation is possible between *Lactuca sativa* and *L. indica*, but that the forms of *Bremia* from the other hosts are confined to their respective hosts. *Bremia* from *Lactuca chinensis* will not infect *L. sativa* or *L. indica*. These findings are considered to show that immunity or susceptibility to a parasite gives good information about the relationships of the host plants. In both *Lactuca sativa* and *L. indica* the

basic chromosome number is 9, and cross-inoculation succeeds; *L. chinensis* has a basic number 16, and on this, and on the reactions to *Bremia*, *Lactuca chinensis* appears to be but remotely related to the other two species of *Lactuca*. Schultze and Röder (1938) reported that *L. scariola* and *L. virosa* react to infection by downy mildew much as did the cultivated lettuce; these two species belong to the 9-chromosome group.

Table 2. *Results of cross-inoculation with* Bremia *on seven species of Compositae*

Source of inoculum	*Lactuca sativa*	*Lactuca indica*	*Lactuca chinensis*	*Taraxacum mongolicum*	*Crepis japonicus*	*Saussurea affinis*	*Sonchus oleraceus*
Lactuca sativa	+	+	−	−	−	−	−
L. indica	+	+	−	−	−	−	−
L. chinensis	−	−	+	−	−	−	−
Taraxacum mongolicum	−	−	−	+	−	−	−
Crepis japonicus	−	−	−	−	+	−	−
Saussurea affinis	−	−	−	−	−	+	−
Sonchus oleraceus	−	−	−	−	−	−	+

+ infection; − no infection.

Factors affecting the size of the sporangia

Schweizer (1919) showed that the dimensions of the sporangia of *Bremia Lactucae* are influenced by the host plant as well as by humidity. As some taxonomists have emphasized the importance of biometric data in dealing with fungi, it seemed worth while to determine the range of variation in the dimensions of sporangia in relation to environmental conditions, and to consider the value of the data to the taxonomist.

For this purpose, *Bremia* was grown on the cultivated lettuce; attention was paid to the effect of temperature, age, and the nature of the host tissue on the dimensions of the sporangia. The effect of temperature was tested by measurements taken from sporangia grown at 10° C., and at 24–28° C. Detached leaves, after being thoroughly washed to remove any sporangia then present on them, were placed in moist chambers for eighteen and for thirty-six hours, and the resulting sporangia sampled and measured. The influence of the host tissue was investigated by comparing the dimensions of sporangia grown on cotyledons and on mature leaves respectively. The results of all these tests appear in Table 3. The measurements (when allowance is made for probable error) show that both temperature and age have significant effects upon the lengths and widths of sporangia, and that there is very little difference between sporangia grown on cotyledons and on mature leaves of the host.

Ecological relations

The behaviour of *Bremia* on the seven hosts in the field was not uniform, for there were differences in developmental history, in the date of appearance and in the duration and extent of infection. These differences were not entirely due to the association of the fungus with the growing season of the host, and it seems likely that there was some difference in the

response of the fungi to environmental conditions. Lettuce is cultivated in the neighbourhood of Chengtu for almost the whole of the year, and its mildew has the longest period of occurrence, generally lasting for ten months, from October to July. A few of the other hosts, *Lactuca chinensis*, *Crepis japonicus* and *Taraxacum mongolicum* are present for almost all the year, except for a short time in the hottest part of the summer, and yet on them *Bremia* is limited in occurrence from late autumn to early spring. *Sonchus oleraceus*, *Saussurea affinis* and *Lactuca indica* are relatively short-lived and therefore are infected for but a short period. Throughout 1943, observations were made every ten days, so that the first and last appearances

Table 3. *Factors influencing the dimensions of sporangia of* Bremia Lactucae *on cultivated lettuce*

	Temperature		
Measurement	10° C.	24–28° C.	Difference
Length: Range	11·4–24·3	10·0–21·5	
Mean	17·95 ± 0·705	16·37 ± 0·795	1·58 ± 0·079*
Width: Range	11·4–22·9	8·6–21·5	
Mean	16·58 ± 1·187	15·17 ± 1·036	1·41 ± 0·111*
Length/width	1·08	1·08	
	Age of sporangia		
Measurement	18 hr.	36 hr.	Difference
Length: Range	8·6–20·0	11·4–21·5	
Mean	14·82 ± 0·820	16·57 ± 0·818	1·75 ± 0·081*
Width Range	8·6–20·0	10·0–21·5	
Mean	14·14 ± 0·851	15·69 ± 1·005	1·55 ± 0·090*
Length/width	1·05	1·12	
	Host tissue		
Measurements	Mature leaf	Cotyledon	Difference
Length: Range	11·4–24·3	11·4–24·3	
Mean	17·95 ± 0·705	17·59 ± 0·940	0·36 ± 0·083*
Width: Range	11·4–22·9	11·4–22·9	
Mean	16·58 ± 1·187	16·65 ± 0·762	0·07 ± 0·101
Length/width	1·08	1·06	

* Significant (D./P.E.$_d$ > 3·2).

of the fungi could be determined; the results of these observations are given in Fig. 4. Usually, *Bremia* is not to be found during the hot season; in July, August and September, though relative humidity is usually at or above 80 %, the high temperature checks the growth of *Bremia*. Very occasionally, during the hot season, the mildew may be found in shady places where the temperature is relatively low and humidity higher than in the open field; once, in August 1943, a heavily infected lettuce was found under a hedge.

As the mildew disappears in the hot season, its manner of over-summering comes into question. Most mildews are narrowly specialized to certain hosts, and it seems very unlikely that there are summer hosts. Weber's

suggestion (1928) that wild plants act as centres of infection from which the mildew spreads to the crops can hardly be accepted. *Bremia* rarely forms oospores and the sporangia seldom survive long enough to serve as sources of infection in the autumn. Angell and Hill (1931) stated that sporangia of *Bremia Lactucae* from lettuce gave 1 % germination after desiccation for thirty-five days. At Chengtu, the high humidity and high summer temperatures greatly reduce the viability of the sporangia; even in March, very few sporangia were alive in a sample taken from cultivated lettuce and exposed on dry slides in the laboratory for 100 hours. If this happens with *Bremia* from lettuce it will be even more difficult for over-summering by sporangia to occur in *Bremia* from other hosts, with a shorter growing season and a longer gap in the life cycle to be covered. The

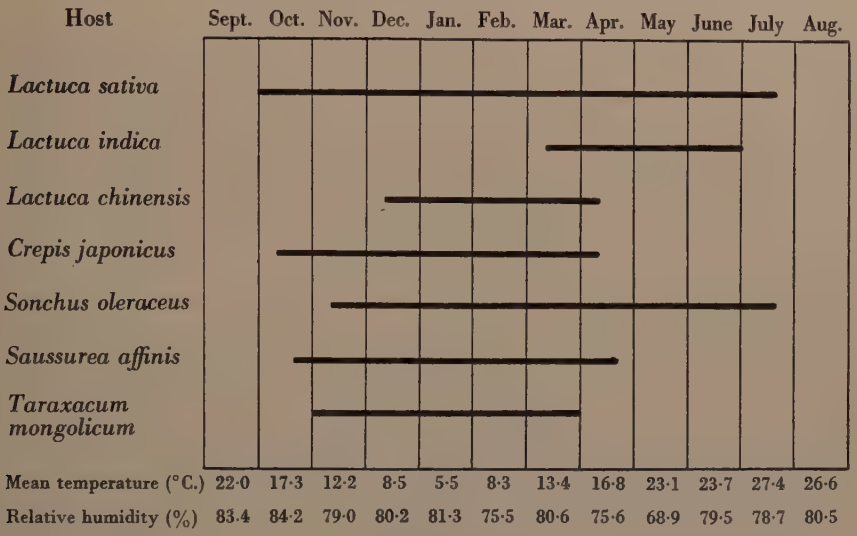

Fig. 4. Seasonal occurrence of *Bremia* on seven species of Compositae in Chengtu, 1943.

occasional appearance in infection on seedlings of lettuce germinated in Petri dishes suggests that these mildews very probably over-summer in infected seeds.

Centaurea Cyanus, *Picris hieracioides* and species of *Cirsium* are rather common around Chengtu, and have been reported as hosts of *Bremia* in other parts of the world, but prolonged search has failed to reveal *Bremia* on these plants at Chengtu.

Discussion

Since Gäumann (1923) published his work on *Peronospora* there has been a widespread tendency to separate the species belonging to this family on very small characters. A number of old and well-known species have been split on biometric data and on specialization to certain host plants, and usually this has been done without experimental evidence. *Bremia Lactucae*

has been recorded on species belonging to twenty-two genera of the Compositae. If all the forms occurring on different genera or even on different species should be proved to be specialized in their parasitism, is it desirable to establish at least twenty-two species to accommodate these forms? If that is done, there will be a great multiplication of names, and taxonomic work will be made very difficult. Moreover, environmental conditions may affect the morphology of the fungus as greatly as does a difference of host. The present work shows that age and temperature can cause statistically significant differences in the dimensions of the sporangia, and further evidence of variation due to environmental conditions is provided by the fact that the published descriptions of these fungi do not agree completely with our observations, even though the hosts are the same.

To satisfy the general requirements of taxonomy, species should be based on readily distinguishable characters. The meaning of the words 'readily distinguishable' is all important, but there is no general agreement about that, and disputes are therefore frequent. As a result of this study of *Bremia*, the fungus from *Saussurea* is considered to be a distinct species because it is easily distinguished from all the others by its large sporangia. Its host plant, *Saussurea*, belongs to the tribe Cynareae of the Compositae, and is widely separated in its relationships from the six other hosts, all of which belong to the Cichorieae; for the fungus from *Saussurea*, the name *Bremia Saussureae* Sawada is accepted. The fungi from the other six hosts are all held to be forms of *Bremia Lactucae* Regel; some show marked specialization to one host, and they may also be separated by morphological characters which are not however very marked. The fungus from *Crepis japonicus* with its long sporangiophores and a tendency to form a preponderance of narrow sporangia, may deserve specific rank, but for the present it is regarded as a form of *Bremia Lactucae*.

The following revision of nomenclature is proposed:

Bremia Lactucae Regel (syn. *B. elliptica* Saw.). On *Lactuca sativa* and *L. indica*.

Bremia Lactucae Regel f. **chinensis** f.n. On *Lactuca chinensis*; forma specialis ex *Lactuca chinensis*; sporangia parvis.

Bremia Lactucae Regel f. **sonchicola** (Schlecht.) comb.nov. (syn. *Botrytis sonchicola* Schlecht.: *Bremia Sonchi* Saw.). On *Sonchus oleraceus*.

Bremia Lactucae Regel f. **Taraxaci** (Ito & Tokunaga) comb.nov. (syn. *Bremia Taraxaci* Ito & Tokunaga). On *Taraxacum mongolicum*.

Bremia Lactucae Regel f. **ovata** (Saw.) comb.nov. (syn. *Bremia ovata* Saw.). On *Crepis japonicus*.

Summary

Bremia was collected near Chengtu, China, from seven genera of Compositae, and the forms from these hosts can be placed in three groups, based on the dimensions of the sporangia. The fungus from *Saussurea* is regarded as a distinct species, *Bremia Saussureae* Saw., the others as *Bremia Lactucae* and forms of that species. Successful cross-inoculations were made between *Lactuca sativa* and *L. indica*, but the other fungi were specialized to their natural hosts.

The taxonomy of *Bremia* is reviewed, and a revision proposed.

Experiments showed that the dimensions of the sporangia could be influenced by temperature and by age. It is suggested that *Bremia* survives the hot part of the summer, when high temperatures prevent its growth, by means of infected seeds.

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THE DISPERSION OF AIR-BORNE SPORES

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(With 6 Text-figures)

I. Introduction

The dispersal of passively air-borne particles, such as seeds, spores or pollen, results in a *scatter* around the point of liberation. The process is influenced by many factors, so unpredictable at first sight that the resulting dispersion pattern might appear to defy analysis. An analysis should be attempted, however, because knowledge of the pattern is fundamental for the understanding and control of the dispersal process itself. The discussion that follows will be based mainly on dry fungus spores in the role of plant pathogens, but it applies to other particles carried passively by wind, such as seeds, pollen (microspores) and respiratory allergens, and has a bearing on the dispersal of some viruses and mutant genes.

Certain facts about the process are widely recognized. The practice of isolating clean plants and crops from sources of disease or foreign pollen depends on the observed fact that the amount of contamination suffered generally decreases the farther away one gets from the source. This was recognized for cereal diseases by Windt (1806, cited from Ramsbottom, 1934), who found that rust on rye was severe near barberry bushes, which are now known to be the alternate host of the fungus: 'These effects are striking and desolating in the distance of ten to twelve paces. I have also perceived them visibly at the distance of 50, 100, 150 paces' and a final attack at 'above 1000 paces'. The scatter pattern is thus recognized as producing, in graphical representation, a gradient of infection. This idea underlies Pape and Rademacher's (1934) proof that in Germany, winter barley contaminates the spring-sown crop with *Erysiphe graminis*, and Bonde and Schultz's (1943) demonstration that in Maine, potato-refuse piles are the principal sources of the contamination of potato fields with *Phytophthora infestans*. The problem is to find whether any general relation exists between these gradients. The problem is statistical because, while the destination of a single spore in a wind eddy is inscrutable, the average distribution of vast numbers of spores over a uniform area and over a period of time offers hope of rational treatment.

Brief mention must first be made of some earlier attempts to formulate such a relationship on abstract grounds. Nägeli (see Stepanov, 1935) concluded that the density of dust particles should fall off inversely as the square of the distance from the source. Kursanov (see Stepanov, 1935) stated that in the absence of wind the number of fungus spores would fall

off inversely as the cube of the distance from the source. Without any proof or reference to other authors, Fischer and Gäumann (1929) state that with linear increase of the distance the chances of infection by rust spores decrease in cubic progression. These formulations appear to rest on the assumption that a passively air-borne particle can be treated like a radiation, passing outwards into space in a straight line until obstructed. However, since our particles are air-borne they cannot radiate in this manner because the air itself is obviously not in process of being continuously generated at all points in the atmosphere and consequently some totally different concept is needed.

Qualitative aspects of the dispersal of fungus spores in air are reviewed by Butler (1917), Gardner (1918), Weston (1923), Stepanov (1935), Craigie (1940), Keitt (1942) and Christensen (1942). For pollen, reference should be made to Rempe (1937) and to Erdtman (1943). The role of air-borne moulds in asthma is reviewed by Durham (1942) and by Morrow and Lowe (1943).

This survey first discusses the nature and magnitude of factors that control the scattering of air plankton. The literature is then examined to see whether the observed distributions of plant pathogens follow any recognizable patterns. Finally, the application of the subject is discussed with special reference to the study and prevention of air-borne diseases of field crops.

II. The factors controlling dispersal

The first stage in dispersal is the liberation of spores or pollen from the structures in which they were formed. The mechanisms of spore discharge in the fungi are the subject of an extensive series of researches by Buller (1909–34). Ingold (1939) has given a concise account of spore discharge in land plants, while Dobbs (1942) gives a classification of spore-dispersal mechanisms in the fungi. The mechanisms for liberating pollen are dealt with by Kerner and Oliver (1895), and more recently by Rempe (1937). After liberation from the plant the spore is operated on by various forces such as gravity, wind currents and electrostatic forces. It will be convenient to consider first those forces acting on a single particle and then to discuss work relevant to groups of spores.

(1) *The fate of an individual spore.* In still air, spores fall slowly under gravity. The open air, however, is never still, and even inside a closed room spores can be carried in feeble air currents and deposited far from the point of liberation. However, the rate at which spores fall in still air has been studied as a factor in distant dispersal and must be considered.

The period after discharge during which a basidiospore, for instance, is undergoing a positive acceleration due to gravity is very short on account of the small mass of the spore in comparison with its area. After a fall of less than one diameter of the spore (10μ) of *Amanitopsis vaginata*, Buller (1909) found that acceleration was balanced by increased air resistance and that the fall continued thereafter at a constant terminal velocity. It is likely that this velocity even decreases if desiccation further reduces the

mass of the spore. Stokes's law described a relation between the size and velocity of fall of a smooth sphere in a viscous fluid in the following terms:

$$V = \frac{2}{9} \cdot \frac{\rho - \sigma}{\mu} g r^2,$$

where V = terminal velocity, ρ = density of the sphere, σ = density of the medium, g = acceleration due to gravity, r = radius of the sphere, μ = viscosity of the medium.

Using as a test object the nearly spherical spores of *Amanitopsis vaginata*, with a density in moist air of 1·02, Buller (1909) observed terminal velocities about 50% greater than expected from Stokes's law. Later (Buller, 1922) this was attributed to the effective size of the spore being increased by a droplet of water which was always found to be excreted and carried away when the spore was discharged from the basidium. Further work showed that on leaving the fungus fruit-body and falling through dry air the spores rapidly lost velocity owing to desiccation, and completely air-dried spores were seen to fall only one-third as fast as fully turgid spores.

That Stokes's law adequately described the fall in air of artificial spheres of wax, mercury, etc., of the same order of magnitude as fungus spores, has also been shown by Zeleny and McKeehan (1910), but they found that spores of *Lycopodium*, *Bovista* and *Polytrichum* fall only about half as fast as predicted by the theory. This they attributed to irregularities on the surface of the spores setting up eddies in the immediate neighbourhood of the particle, while Stokes's law applies to non-turbulent conditions. Rempe (1937) has suggested that, because of surface irregularities, pollen grains may become coated with a stationary surface layer of air which increases their effective diameter.

Exact prediction of the terminal velocity of a spore is hindered by the difficulty of determining its density (which in turn depends on its hydration), and by deviation from the ideal smooth spherical form. In Fig. 1. are plotted the terminal velocities of spores and pollen grains observed by various workers, together with the velocity to be expected from Stokes's law for a sphere of density 1·00. The sizes of asymmetrical spores are represented on the graph as the geometric mean of the short and long axes. Assuming $\rho = 1{\cdot}00$, σ negligible, $\mu = 1{\cdot}8 \times 10^{-4}$ (viscosity of air), $g = 981$ in c.g.s. units, we have $V = 0{\cdot}0121r^2$, where r is the *radius* of the sphere in microns, and V is in cm. per sec.

According to Erdtman (1943), the observed terminal velocities of air-dry pollen are usually somewhat higher than the expected values. Pohl (cited from Erdtman) found that the specific gravity of pollen grains varied from 1·161 for *Typha latifolia* down to 0·391 for *Pinus sylvestris*. Buller (1909) found the density of hydrated spores of Agaricaceae to be about 1·02, while for spores of *Polytrichum*, Zeleny and McKeehan (1910) recorded a value as high as 1·53. In general, the observed terminal velocities of pollen are greater than those of fungus spores, varying from nearly 40 cm.sec. for *Abies*, down to about 1·5 cm.sec. for *Alnus viridis*. Fungus spores tend to fall more slowly, and vary from nearly 3·0 cm.sec. for *Helminthosporium*

sativum, down to 0·05 cm.sec. for species of *Lycoperdon*. The biggest deviations from expectation are shown by the slow-falling pollen of *Picea* and *Pinus*, which have large air sacs, and by the relatively fast-falling caudate spores of *Bovista plumbea*. In general, it may be said that the terminal velocity of roughly spherical spores is of the order expected from Stokes's law (Fig. 1).

McCubbin (1918), Ukkelberg (1933) and Stepanov (1935) allowed spores of rusts and other fungi to fall in columns of air in vertical cylinders,

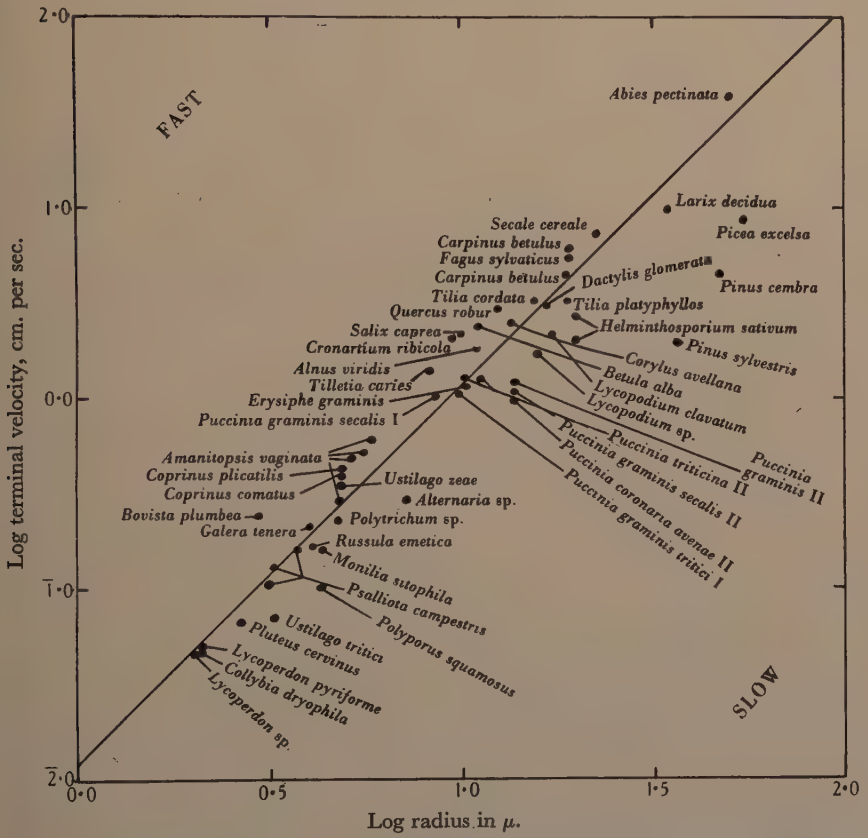

Fig. 1. Observed terminal velocities of fall of spores and pollen grains in cm. per sec., plotted against radius in microns (if highly asymmetric the geometric mean of long and short axes is taken) from data of Buller, Zaleny and McKeehan, McCubbin, Ukkelberg, Stepanov, Rempe, Yarwood and Hazen, Christensen, and Erdtman. The straight line represents expected velocity of fall of a smooth sphere of density = 1·00, according to Stokes's law.

and deduced the terminal velocity from the numbers of spores deposited at the foot of the column at successive intervals after liberation of the spores. In general, both McCubbin and Ukkelberg obtained data of a similar type, and a graph of the number of spores reaching the bottom of the tube in successive time intervals showed a negative skew distribution.

Part of the skewness of the curve was shown by Ukkelberg to be due to clumps of spores falling with a high velocity, but it is equally clear that uredospores and aecidiospores of rusts also show skewness due to an excess of single spores falling very slowly. Unfortunately, neither McCubbin, Ukkelberg nor Stepanov measured the spores to find whether the first to arrive at the bottom of the column of air were larger than those arriving at the end of the run, and the effect may have been due to an experimental error caused by eddies in the column of air. Ukkelberg showed that differences in the rate of spore fall of uredospores and aecidiospores of *Puccinia graminis tritici* and *P.g. secalis* were probably due to differences in size, but it remains to be shown whether differences in the terminal velocity within a population are also due to differences in size. Ingold (1939), studying the violently discharged spherical spores of *Conidiobolus villosus* whose diameters vary from 15 to 48 μ, found that in still air, as might be expected from Stokes's law if the spores were all shot off with the same initial velocity irrespective of size, the spores were discharged to horizontal distances proportional to the square of their radius.

Stokes's law applies only to smooth spherical particles. Most fungus spores are not isodiametric but more or less elongated; the ascospores of *Ophiobolus graminis* for instance have a length about twenty times their width. Buller (1909) observed that elongated spores tend to fall horizontally and that the final position which the spore took up in air was, as would be expected, such that the greatest surface was presented to the resistance of the air. Under experimental conditions, however, *Erysiphe graminis* with conidia measuring $32 \times 20\,\mu$ was found by Yarwood and Hazen (1942) to behave anomalously.

For a spore of a given volume any elongation will expose a relatively larger surface and so decrease the rate of fall to a value below that expected for a sphere. Very few tests appear to have been made on the terminal velocity of markedly asymmetrical spores, interest having been focused on spherical particles by Stokes's law. McCubbin (1944) deals with the fall of non-spherical spores and stresses the need for more empirical data with precautions against eddies. The fall of *Helminthosporium sativum* has been studied by Stepanov (1935) and Christensen (1942) who obtained values of 2·78 and 2·0 cm.sec. respectively, for spores measuring $68 \times 24\,\mu$ and $75 \times 20\,\mu$. It can be calculated that a cylinder of such dimensions would approximately equal the volume of a sphere of 40 μ diameter with an expected terminal velocity of about 4·8 cm.sec. Christensen also tested spores of *Alternaria* sp. $20 \times 10\,\mu$, and observed a speed of 0·3 cm.sec. This, it may be suggested, is nearer the speed one would expect if the spores fell with their long axes vertical, as some *Alternaria* spores might do owing to the feathering effect of the elongated beak of the spore. I have observed that the caudate spores of *Bovista plumbea* are orientated in this way during fall. More observational data are evidently needed before it can be assumed that all elongated spores fall more slowly than would spheres of the same volume.

The effect of one of the forces acting on spores in air can now be summarized. The vertical effect of gravity results in a terminal velocity

of fall of the order of 1 cm.sec. According to the size and shape of the spore the speed is observed to vary from 0·05 cm.sec. for *Lycoperdon* to 2·8 cm.sec. for *Helminthosporium sativum*, and 9·0 cm.sec. for pollen of *Picea excelsa*. Within an individual species the speed may vary by 100%, as with Ukkelberg's observations on *Puccinia graminis secalis* (0·73–1·47, with a mean of 1·02 cm.sec.), possibly owing to variations in the size of individual spores. Elongated spores sometimes do and sometimes do not fall slower than would spherical particles of the same volume, possibly because of mechanisms affecting orientation.

(2) *Minor forces acting on spores.* The basidiospores of the mushroom and some other fungi have been shown by Buller (1909) to carry small electric charges when falling in air. Little is known about the phenomenon, and its effect is probably negligible except when the spore is within about a millimetre of another body. The origin of the charge, its effect over very short distances, and its relation to the vertical potential gradient in the atmosphere, which is said to average about 150 V. per m., might repay future investigation. It is also known that small particles tend to move down a temperature gradient (Cawood, 1936; Watson, 1936), and that forces exist causing particles, at least up to 2 μ in diameter, to be repelled by a hot surface and attracted by a cold one. Smoke particles and *Lycopodium* spores are also known to move away from light (photophoresis, Whytlaw-Gray & Patterson, 1932).

(3) *Wind.* Besides the vertical force of gravity, spores are also acted on by wind which can be considered as a force acting horizontally. The mean velocity in England is considered to be about 5 m. per sec. (Sutton, 1932). Wind records usually refer to a standard anemometer exposed at 10 m. above the ground. Wind velocity tends to increase with height, and the speed at 2 m. would be only about 0·78 of that at the standard height. Summaries of wind-frequency data in the detail required for understanding the present problem are seldom given, but tables of wind frequency at 7 h. and 18 h. for Lerwick, Shetland, and for Scilly, England, each based on 3625 observations, are given by Bilham (1938). At both these coastal stations over 96% of the observations showed winds above 0·3 m.sec. The highest frequency class was 3·4–5·4 m.sec. at Lerwick, and 5·5–7·9 m.sec. at Scilly. As an example of wind velocity frequencies at an inland station the hourly readings for the year 1937 for the anemometer at Kew, England, have been tabulated from data published by the Meteorological Office (1939). It was found that at Kew nearly 90% of the hourly means were 1·0 m.sec. and upwards, and that for over half the time the speed was 3·0 m.sec. and upwards. Wind speeds therefore are commonly 300 times, and usually at least 100 times as great as the rate of fall of spores under gravity, so it is likely that wind velocity is a major factor in controlling spore dispersal. Wind speed may also play a part in altering the number of spores or pollen grains liberated by the plant, as was realized by Stepanov (1935). Many Hymenomycetes shed their spores irrespective of wind conditions, but others, like puff-balls and probably many rusts and dry-spored *Fungi imperfecti*, liberate more spores the greater the speed of the wind. Many flowering plants have mechanisms which ensure that

pollen is not liberated into air moving at less than a critical speed (Kerner & Oliver, 1895).

(4) *Spore dispersal as the resultant of horizontal and vertical forces.* Previous estimates of the probable limits of spore dispersal have usually been based on the trajectory of an individual spore considered as the resultant of its vertical fall under gravity and its horizontal transport by wind. Data on the slow speed of fall have been quoted as evidence that spores may be carried for great distances.

McCubbin (1918) considered that 'the general problem of spore dispersal is vitally a question of maximum dispersal distance', a view that is contested in this paper. He accordingly concentrated most attention on the relatively few spores in his experiments, described above, which fell most slowly and were therefore likely to be carried farthest by air currents. It was calculated that spores falling at 0·8 cm.sec., and liberated from a height of 8 ft. would be carried by a 30 mile per hour breeze for $2\frac{1}{2}$ miles before settling. It was realized that deflexions of the wind and rising masses of heated air would often tend to carry the spores upwards and thus increase the dispersal distance (see Buller, 1924, p. 560). Similarly, Christensen (1942) calculated the approximate theoretical dispersal distance of spores falling under gravity from a height of 1 mile in a 20 mile per hour wind, and estimated that an *Alternaria* spore would travel 2900 miles before reaching the ground.

Table 1. *Percentage of total number of spores trapped at various distances from the point of liberation of a mixed cloud of* Tilletia *and* Bovista (from data by Stepanov, 1935)

	Distance in metres			
Species	5	10	20	40
Tilletia caries	74·1	17·8	7·4	0·7
Bovista plumbea	74·4	19·9	4·9	0·8

Such estimates are based on highly artificial conditions in which the spore is supposed to be raised to a given height and then dropped through a steady stream of air moving horizontally. Stream-line conditions do not as a rule extend more than a millimetre or two above the surface. There is some experimental evidence that the size of a spore and the velocity of its fall have little effect on the dispersal distance. In an experiment conducted in the open air Stepanov (1935) liberated a mixture of spores of *Tilletia caries* and *Bovista plumbea* whose mean diameters and terminal fall velocities he had previously determined as 17 and 5·6 μ and 1·41 and 0·24 cm.sec. respectively. The spores were trapped on the ground at various distances from the point of liberation and at various angles to the prevailing wind. The experiment is discussed fully below, but data summarized in Table 1 show that the relative density of deposit of spores of both species decreased with increasing distance at almost precisely the same rate, in spite of the fact that spores of *Tilletia* fell about six times as fast as those of *Bovista*. In Table 1 the number of spores trapped at each distance is given as a percentage of the total number of spores of each species trapped. The fact

is that the behaviour of an individual spore is unpredictable with our present knowledge. Further progress cannot be made until attention is turned from the fate of the individual spore to that of a group of spores. The methods cited above omit consideration of a third essential factor in spore dispersal, the turbulence of the air.

(5) *The fate of a group of spores.* The foregoing discussion considered the motion of a spore in terms of a vertical component of the order of 1 cm.sec., and of a larger but more variable horizontal component varying from 30 to 2500 cm.sec., with a mean near 300 cm.sec. These conditions only even approximately describe the motion in the comparatively rare cases of non-turbulent air movement, such as under extreme temperature inversions, or katabatic flow (Cornford, 1938).

Watching the drift of smoke from a bonfire or a factory chimney will convince the observer that wind, instead of being a steady streaming motion, is characteristically turbulent. According to Brunt (1934) there are usually present in the atmosphere large numbers of small-scale eddies whose periods are of the order of 1 sec., and at least two-thirds of the eddying energy is associated with eddies of periods of less than 5 sec. The action of the numerous eddies of varying size on the very numerous spores produced from plant sources makes regularity in the dispersal pattern possible.

Turbulence can be mechanical or thermal (Durst in Giblett, 1932). Mechanical turbulence is caused by friction between the wind and the ground over which it passes, and the gustiness developing depends both on the roughness of the ground and the speed of the wind. Thermal turbulence depends on convection currents set up when short-wave radiation from the sun, passing unabsorbed through the atmosphere, warms the ground which in turn warms the layer of air in contact with it by emitting a longer radiation. Under these conditions there may be a rapid decrease (lapse) of temperature with height in the atmosphere and convection currents are set up leading to turbulent mixing of the lower layers of the atmosphere. In clear weather thermal turbulence is at a maximum soon after midday, while on a clear night thermal turbulence may die away completely if cooling of the ground by radiation leads to an inversion of temperature gradient (an increase of temperature with height instead of the usual decrease), in which there is no tendency for lower layers of air to ascend. For an elementary account of this subject reference should be made to Sutcliffe (1940), Brunt (1942), or for greater detail to Brunt (1934).

The effect of turbulence is that a puff of spores or pollen, as well as being carried along in the general direction of the wind, is continually being diluted as one eddy or another mixes the mass of air in which the spores are suspended with other masses of air. Eddying thus diffuses the spores in all directions and, as time passes, so the density of the spore cloud diminishes. Some visual impression of the magnitude of the effect of eddies in diffusing a cloud may be obtained by watching the increasing width of a smoke trail as it drifts away from a chimney. It will become obvious from the subsequent discussion that the magnitude of this diffusion

is such that its effect on a spore cloud is much greater than the effect of gravity.

(6) *The spore cloud regarded as a suspension.* The diameters of air-borne spores and pollen grains may be taken as varying around 10 and 20 μ respectively. This is approximately the magnitude of the droplets forming cloud and fog (Simpson, 1941, 4×10^{-4} to 2×10^{-3} cm.) which are obviously in a state of suspension and show little tendency to sink until they have aggregated. With knowledge of the small speed of spore fall and the large stirring effect of atmospheric turbulence it is tempting to regard the spore cloud also as a suspension.

Like most other suspensions the spore cloud will tend both to precipitate under gravity and to be stirred up by diffusion. The concentrations of spores at different heights in the atmosphere will be the result of the interaction of these two forces. The numbers of spores and pollen grains occurring at different altitudes have been investigated quantitatively in Canada and Germany, and we can make use of the data to see whether the distributions found correspond with known values for terminal velocity and turbulence. The treatment given here is adapted from Schmidt (1925), who shows that for a stable condition, when the number of particles falling under gravity across any horizontal boundary is compensated for by the number of particles moved upwards by diffusion, the concentration of particles in the air decreases exponentially with increasing height according to the equation

$$S = S_0 e^{-Vz/K} \quad \text{or} \quad \log_e S_0/S = V(z/K),$$

where S_0 = concentration at height $z = 0$, V = terminal velocity of fall, K = Taylor's 'eddy diffusivity' constant (assumed invariable with height) and used here in place of Schmidt's 'Austausch' coefficient, A.

During an epidemic of wheat rust in Manitoba in July and August 1930, Peturson (1931) trapped spores at different altitudes in eight aeroplane ascents. The average numbers of spores caught per square inch of trap surface (presumably with comparable exposure times) were: 1000 ft. 10,050 spores; 5000 ft. 1180 spores; 10,000 ft. 28 spores; and 14,000 ft. 11 spores. By substitution in the previous equation we can calculate K, and taking extreme heights find $K = 5{\cdot}8 \times 10^4$, if $V = 1$ cm.sec.

Hubert (1932) trapped spores during two flights at the time of an epidemic of yellow rust of wheat at Halle in Germany. During the second flight, for which data are more extensive, the numbers of spores trapped per square centimetre per minute exposure at various heights were: 30 m. and less, 1418 spores; 400 m. 683 spores; 600 m. 336 spores; and 800 m. 82 spores. Substitution of extreme values in the equation gives $K = 1{\cdot}5 \times 10^4$. The vertical gradient of spore concentration, but with smaller numbers trapped, has also been observed by Stakman and others (1923), Dillon Weston (1929), and Newhall (1938).

According to Brunt (1934, p. 224) meteorological data at heights up to 1000 m. indicate values for K ranging from $1{\cdot}0 \times 10^3$ over the sea during a temperature inversion up to a normal value of 10^5 under average conditions. The distributions of rust spores observed by both Peturson and

Hubert confirm the assumption that spores are present in the air in the form of a stable suspension in which the terminal velocity is balanced by an eddy diffusivity of the usual order of magnitude.

Similar values for K were indicated when tree pollen was trapped over German forests in spring during a series of aeroplane flights by day and by night (Rempe, 1937). For a full discussion of the meteorological conditions prevailing during the individual flights and their effects on the vertical pollen distribution reference should be made to Rempe's original paper. In general, with light to moderate windy weather and with cumulus clouds at about 2000 m., the pollen concentration decreased only slightly up to 1000 m., and the maximum number of grains might occur as high as 200 or even 500 m. This was regarded as a sign of a complete inversion of air masses. A similar distribution also occurred under high-pressure conditions without clouds but with strong thermal turbulence. On the other hand, conditions associated with a stratified cloud layer and high wind velocities showed a marked decrease of pollen with height. In night flights, the maximum number of grains was often reached at a height of about 200 m., that is, above the temperature inversion which often arises at night. Generally there was at night a more pronounced decrease in the numbers trapped at increasing heights than by day. The total numbers trapped at heights were also lower by night than by day.

The mean number of pollen grains trapped per 1·275 sq.cm. of trap surface per 20 min. flight computed from Rempe's data for all flights for which records extended up to 1500 m. was as follows:

Altitude (m.) ...	10–40	200	500	1000	1500
Day flights	904	849	852	581	267
Night flights	577	560	283	85	45

These records include pollen grains of various species, but taking $V=3$ cm.sec. as a moderate value for speed of fall of pollen grains it can be shown that, for altitudes above the region affected by strong thermal turbulence and temperature inversions, $K=2{\cdot}6\times10^5$ for day flights, and $1{\cdot}6\times10^5$ for night flights.

In addition to counting the total number of grains, Rempe also analysed the grains by species and by size. Usually it was only under the most stable atmospheric conditions at night that any marked sorting out of pollen grains according to size was observed at the different heights; usually the proportions of different sizes were the same at all altitudes, giving convincing evidence of the normally greater importance of turbulence than of gravity on spore distribution. As an example of the sorting out of grains of different species which was occasionally observed, data from one day flight (A6) may be cited. Rempe found: At 2000 m.: *Betula* 73·3%; *Carpinus* 10·0%; *Fagus* 3·3%; and other species 13·4%. At 10–40 m.: *Betula* 29%; *Carpinus* 55·0%; *Fagus* 11·5%; and others 4·5%. Within a single species grains of different sizes were sometimes sorted out as in the night flight (A10) when the mean diameters of *Betula* pollen grains were: 1000 m. 23·0μ; 800 m. 24·5μ; 500 m. 26·7μ; 200 m. 27·5μ; 10–40 m. 27·1μ. Evidently it is only under very low conditions of turbulence that

the differential effect of gravity on pollen grains of different sizes comes into prominence.

From this evidence it seems appropriate to consider the spore or pollen cloud as in suspension in air. At heights of about 1000 m. and upwards the distribution agrees well with that expected from known values of terminal velocity and turbulence. Nearer ground level, however, the suspension tends to become more uniform owing to the intermittent stirring of the lower layers by strong mechanical and diurnal thermal turbulence. As Brunt (1934) points out, the effect of surface turbulence becomes negligible above 1000 m. The result of this stirring, as Horne (1935) has shown by trapping fungus spores over orchards for short periods of time, is that over small areas, micro-organisms are distributed at random in the air. Evidently the observed vertical distribution of air plankton depends on turbulence. Similarly, Kalmus (1936) has demonstrated that turbulence of the medium is also a necessary condition for the existence of plankton in water.

(7) *Spore deposition.* If it is appropriate to regard the spore cloud as a suspension rather than as a shower of particles falling under gravity, the question arises: by what process do they come back to earth?

'When a fluid flows over a solid boundary the portions of the fluid in immediate contact with the boundary are at rest, and there is a thin layer of fluid at the boundary across which there is a rapid increase of velocity, and within which the motion is laminar. The "boundary layer" is a time-mean phenomenon and it is not to be supposed that this layer is always constituted of the same fluid. The turbulence which may prevail at some distance from the boundary will from time to time break through the layer, carrying away portions of the fluid which instantaneously constitute it, but as soon as the individual eddy has removed a portion of the boundary layer normal processes will tend to build it up again' (Brunt, 1934). Above this boundary layer wind velocity tends to increase with height according to some fractional power law.

One of the major problems solved by those land plants that rely on air movement for the dispersal of spores is that of getting the spores away from the surface where they are formed, across the boundary layer of still or non-turbulent flowing air, and into the general circulation of the atmosphere. The adaptation evolved by most Ascomycetes consists in a mechanism for violent discharge of the spores across this layer, and cup fungi by 'puffing' may achieve a ceiling of several inches. Many Basidiomycetes and flowering plants raise the reproductive organ to as great a height as possible, and then drop the spores into the freely moving and turbulent air layers below. Once out of the calm layer of air close to the earth's surface the spores can be freely transported by wind, and the spore cloud is diluted by eddies as it travels. Speed of fall probably plays only a small part in this stage of the dispersal process. But an eddy may at any time bring a spore down into the relatively still ground layer or even to the non-turbulent boundary layer. When a spore is carried down by an eddy into still surface air the effect of gravity would predominate, and here too, if anywhere, the electrostatic forces might be expected to play

a part. In deposition the spore has once again to cross the quiet boundary layer. Here, as Bagnold (1941) points out, dust particles sink into a viscid surface layer of air and are out of the reach of eddies, 'the surface of the ground acts as a sort of dust trap'.

There seem to be no quantitative tests on the deposition of fungus spores, but studies on pollen deposition with special reference to pollen analysis have been made in Germany. Rempe (1937) used two methods for trapping pollen near the ground. Pollen deposition (*Niederschlag*) was measured on horizontal vaselined slides about 1 cm. above the ground. Pollen drift (*Anflug*) in free air was measured by small brass tubes, 14 mm. wide by 45 mm. long, wrapped around the surface with vaselined cellophane, and hung vertically from trees or stakes at the required height (not with cellophane across the ends of horizontal tubes as stated by the Committee on Apparatus in Aerobiology, 1941). In any given position pollen drift was usually much greater than pollen deposition. For instance, at 100 m. in a horizontal direction from a hazel bush the pollen drift at a height of 3 m. was over twenty-five times as great as pollen deposition on the ground. In another series of tests carried out on the level roof of the Göttingen Botanical Institute, values for drift and deposition were obtained over a whole month (Table 2). The fact that deposition was

Table 2. *Pollen 'Drift' and 'Deposition' at Gottingen*

Number of grains per sq.cm. of trap, 1–30 May 1935 (Rempe, 1937).

	Pollen drift 2 m. above roof	Pollen deposition at roof level
Day	23,525	11,200
Night	4,675	6,800
Total of day and night	28,200	18,000
Night as percentage of total	16·6	37·8

smaller by night than by day is interpreted here as due to lower turbulence under night conditions, causing fewer grains to be brought down by eddies to the boundary layer over the horizontal trap. The lower drift values at night do not necessarily indicate a smaller amount of pollen in suspension in the air at night because Rempe's observed drift (spores brought against a sticky surface) will depend on the speed of the wind and its turbulence as well as on the spore content. Actual counts of grains or spores in a measured volume of air would be necessary to establish differences in the number of particles in suspension, but Rempe's aeroplane data, referred to above, indicate that the pollen content by night was only half that during the day. The data in Table 2 show very clearly that by day drift is 50% greater than deposition, while at night, deposition gains in relative importance and is twice as great as drift, apparently on account of decreased turbulence leading to a relative importance of fall under gravity.

By trapping pollen of low-growing plants by both methods Rempe also

showed that there is a zone extending for a few centimetres above ground level which is characterized by predominantly falling pollen.

Rempe also observed that rain had a marked effect in removing pollen from the air, but whether the grains acted as condensation nuclei, or whether they were removed by contact with raindrops falling through the suspension, was left open. In one example, 0·31 grain was trapped per sq.cm. per 4 min. exposure before a thunder shower, during the shower 1·90 grains were deposited, and immediately after the shower only 0·15 grain was deposited, indicating that the pollen content of the air had been halved. During one spell of rainy weather the number of grains trapped decreased steadily to one tenth of its initial value in the course of 2 days. Rain must thus set a limit to the otherwise indefinite process of dispersal by periodically washing the spore load out of the air. For the smaller particles of smoke it has been shown that rain is the principal factor in bringing about deposition, but it must be regarded as incidental for wind-borne pollen and spores, since with many species of plant they are not liberated during rain.

The spore cloud is appropriately regarded as in suspension, and while in process of dispersal in the free air above the ground, spore fall can probably be ignored. In its transport by wind the cloud is acted on by eddies which not only maintain the vertical concentration gradient, but also dilute the travelling spore cloud, which would tend ultimately to a uniform horizontal distribution over the earth's surface if the numbers were not depleted by deposition and by washing out by rain. The factors dominating the actual process of dispersal reduce to two: wind transport and eddy diffusion.

(8) *Eddy diffusion.* The importance of turbulence for dispersing seeds, pollen and spores was first suggested by Schmidt (1918, 1919 and 1925) who derived an equation for the transfer of small particles in the air, an equation which is similar to those for the conduction of heat or for molecular diffusion. A general discussion of this work and the derivation of similar equations for the transfer by eddies of heat, momentum and matter which have been developed by Taylor (1915) and by Richardson (1920) is given by Davies and Sutton (1931), and by Bosanquet and Pearson (1936).

In dealing with the work of Schmidt the monograph (1925) will be used, as the earlier paper (1918) contained an error which was corrected later (1919). Schmidt considered the dispersal of a quantity Q of spores liberated into the air at an instant of time from a fungus growing on a tree. Temporarily it was supposed that the effect of gravity on the spores could be ignored, and it was assumed that each spore remained in a small volume of air and moved with it. By reason of the perpetual mixing of the air by eddying the individual spores become separated from one another. The strength of turbulence determining this is measured by a parameter termed by Schmidt the 'Austausch' value, A. On the basic assumption that the flux of spores across a small layer of air, height δz, is proportional to the gradient of concentration across the layer, and that the increase of spores in the layer is the difference of flux across the two boundaries,

Schmidt considered that changes in the spore content s of the air at a height z above the point of liberation after time t would be given by

$$\frac{ds}{dt} = \frac{A}{\rho}\frac{\partial^2 s}{\partial z^2},$$

where A = the *Austausch* value, ρ = the density of the air. Thus A/ρ replaces the coefficient of thermal conductivity in the heat conduction equation. The integrated form of this is given by Schmidt as

$$S = \frac{Q}{2\sqrt{[(A\pi t/\rho)]}} \exp\left[-\frac{z^2}{4(A/\rho)\,t}\right].$$

Here s gives the distribution of spores in the different layers above the point of origin at time t, and equally in the absence of wind or gravitational pull, it gives the lateral and downward distribution due to turbulent mixing. The spores are normally distributed about the point of liberation with a standard deviation given by $\sigma = \sqrt{(2At/\rho)}$. Schmidt next considered what fraction q/Q of the spores occur at time t above a height z, and extended the treatment to include particles with a speed of fall c in a wind of velocity v cm.sec. The treatment is mainly of historic interest and need not be repeated here. As an example of the method, Schmidt calculated the theoretical horizontal distribution of fruits of the dandelion, *Taraxacum officinale*, with an observed velocity of fall of $c = 10$ cm.sec., in an atmosphere with turbulence given by $A = 20$, and density $\rho = 1{\cdot}293 \times 10^{-3}$, and estimated that 1/100 of the fruits would be carried to a distance of at least 10·1 km. Small (1918), indeed, considered that a wind of only 1·97 miles per hour would carry dandelion fruits to any distance, but this extraordinary result was obtained by neglecting the effect of gravity in the argument and eliminating its effects in the experiment. Defining a 'mean limit of dispersal' as the distance beyond which only 1/100 of all particles travel, Schmidt calculated the following mean dispersal limits from observed terminal velocities of spores and pollen: *Bovista* 460,000 km.; *Polytrichum* 19,000 km.; *Lycopodium* 330 km.; *Pinus silvestris* 40 km.

Similar equations for eddy diffusion had been developed by Taylor (1915) and Richardson (1920), and their application to the scattering of smoke was soon made by Roberts (1923). In these equations some such coefficient as the eddy diffusivity, K, corresponds to Schmidt's A/ρ in similar heat-conduction equations.

Davies and Sutton (1931) pointed out that observed values of A varied from 10^{-2} to 10^{2}, and K from 10^{3} to 10^{11} in c.g.s. units, and it therefore appeared that the 'Fickian' heat-conduction equations do not adequately describe fluids in turbulent motion, and that something more than a scale difference is present. These considerations led Sutton (1932) to put forward a theory of eddy diffusion in which the size of the effective eddy was assumed to increase with the distance travelled by the cloud, instead of remaining constant at all distances as in former theories. Sutton showed that earlier theories assume that the size of eddies effective in diluting the cloud do not vary no matter how widely the particles are dispersed.

On the contrary, he states: 'It is clear to anyone who has watched smoke diffusing that the particles start off at first under the influence of small local eddies, but that at greater distances from the source the scatter is such that the relative motion of the particles is dominated by the larger eddies....In the atmosphere we have a state of affairs in which the agents of diffusion are eddies of all sizes, ranging from the minute convectional whorl to the cyclonic depression. When the particles are closely packed together the large scale eddies will have little or no influence on the rate of diffusion, but when the stage is reached that the particles are widely separated the influence of the smaller sized eddies will become less and less, and the relative motion of the particles, and thus the rate of growth of the cluster, will be determined solely by the larger eddies' (Sutton, 1932, p. 145).

Sutton assumed that the correlation coefficient R_ξ between the motion of a particle at one instant and at a time ξ sec. later varies as an inverse power of the distance travelled by the cluster. (R_ξ behaves like $([u]\xi)^{-n}$, $n>0$). Developing an equation for correlated motion in a fluid, originated by Taylor (1922), Sutton found that with a correlation coefficient of the form proposed the standard deviation of the particles would be different from that given by Schmidt's equation. If σ denotes the standard deviation of the particles from their mean position Sutton found that $\sigma^2=\frac{1}{2}C^2(ut)^{2-n}$, where $0<n<1$, and $u=$ mean speed of the wind. (In what follows $2-n$ is usually denoted by m, and ut replaced by the distance travelled, x.) Here C is a new coefficient of diffusion replacing the K of older theories, and m is a parameter depending on conditions of turbulence.

Table 3. *Observed values of parameters of diffusion equation* (Sutton, 1932)

Author reference	Objects observed	Mean C (cm.)$^{\frac{1}{2}}$	m
Richardson and Proctor, 1926	Balloon competitions on Brighton beach (diffusion over hundreds of kilometres)	0·92	1·75
Richardson, 1920	Smoke from continuous point source (diffusion over tens of metres)	0·6	1·75
Sutton, 1932	Expansion of anti-aircraft shell bursts:		
	At height of 945 m.	0·088	—
	At height of 5400 m.	0·03	—
Defant, 1921 (cited from Sutton, 1932)	Trajectories of European cyclones	1·68	2

The range of values obtained by Sutton for C and m by calculation from various sets of data are shown in Table 3. The relatively constant values of C, compared with the widely divergent values of A and K referred to above are taken as evidence that Sutton's theory gives a closer approximation to the facts of turbulent diffusion than do the earlier theories.

The observed decrease of C with height was expected because at great heights conditions are unfavourable for the formation of eddies. Values for m appear to increase with longer sampling periods, and Sutton suggests that m itself is a function of time. In taking continuous observations over a long period on the density of a cloud he suggests that the random element may become smoothed out so that over a sufficiently long period

$m=2$, and C would become $\sqrt{2}$. These possibilities should be borne in mind when the density formulae described below are applied to some biological data where the sampling period is very long. In a later paper, Sutton (1934) found that in the absence of thermal turbulence the normal value of $m=1{\cdot}75$, but that with convection, m increases. The quantity m is an indicator of the degree of turbulence of the medium and is to a first approximation independent of the mean wind velocity. It is primarily affected only by those factors which tend to damp out or enhance turbulence, such as the vertical temperature gradient and the roughness of the surface. Under conditions of extreme turbulence (temperature decreasing with height) m might approach its upper limit of 2, while with the greatest temperature inversions, in which turbulence is damped out, $m=1{\cdot}24$ as a lower limit.

Expressions for the density in a cloud emitted from various types of source were deduced by Sutton (1932), and for the analogous heat-conduction equations, reference should be made to Carslaw (1921). Bosanquet and Pearson (1936) deduced formulae for smoke and also for dust, in which the effect of gravity in causing precipitation was taken into account. The following conditions considered by Sutton in which the speed of fall of the particles is negligible are believed to be more appropriate to the dispersal of fungus spores:

(*a*) *Instantaneous point source*, such as a puff of Q g. of smoke emitted at an instant of time. Here the origin of the co-ordinates is taken at the centre of the moving puff, and the density of the cloud χ is given by the equation

$$\chi = \frac{Q}{(\pi)^{\frac{1}{2}} C^3 (ut)^{\frac{1}{2}m}} \exp\left\{-\frac{r^2}{C^2(ut)^m}\right\},$$

where r = distance from centre of cloud, u = mean wind velocity.

(*b*) *Continuous point source*, such as a factory chimney emitting Q g. per sec. Here, to obtain an integral that can be handled conveniently, the assumption is made that the spread of smoke laterally and vertically is small compared with its spread down wind. The origin of co-ordinates is taken at the point of emission, and Ox is the direction of the mean wind of u cm.sec. When emission has been in progress long enough for the density distribution to reach a steady state the density is given approximately by

$$\chi = \frac{Q}{\pi C^2 u x^m} \exp\left\{-\frac{y^2+z^2}{C^2 x^m}\right\}.$$

The cross-wind density shows a normal distribution of particles. On the axis of the cloud ($y=z=0$) the concentration is given by the simpler expression

$$\chi = \frac{Q}{\pi C^2 u x^m},$$

and since according to the theory, m cannot exceed 2, the fall off in density on the axis of a point-source cloud cannot be more rapid than the inverse square, no matter how turbulent the motion may be.

(*c*) *Continuous line source at right angles to the mean direction of the wind*, emitting Q g. per sec. per cm., and assuming the line to be of infinite length

$$\chi = \frac{Q}{\sqrt{(\pi)\, Cux^{\frac{1}{2}m}}} \exp\left\{-\frac{z^2}{C^2x^m}\right\}.$$

Values obtained by Sutton suggest that as a rough and ready rule a line behaves as an infinite line for distances of travel up to four times its own length. For points on the xOy plane

$$\chi = \frac{Q}{\sqrt{(\pi)\, Cux^{\frac{1}{2}m}}}.$$

III. Horizontal dispersion of spores

An apparently unique set of data obtained by Stepanov (1935) fortunately makes it possible to test the fit of Sutton's theory of eddy diffusion to spore transport.

Stepanov used artificial sources of spores liberated at a point in the open air, and trapped the spores on glass slides coated with glycerine jelly placed on the ground at various distances from the sources and in various directions relative to the prevailing wind. At the end of the experiment cover-glasses were placed on the slides, and the number of single spores per unit area was counted (spore clusters were disregarded).

In Exp. 1 (28 July 1933), on a lawn near the middle Nevka River, Elagin Island, Leningrad, approximately $1{\cdot}2 \times 10^9$ spores of *Tilletia caries* were disseminated into the air through gauze, at a height of about 0·8–1·2m. above the ground. According to anemometer readings the wind varied from 0·5 to 4·0 m.sec., but sometimes fell off to a complete calm; its direction was also variable. Two glass slides were placed at each locus and the numbers of spores trapped are shown in Table 4.

Table 4. *Results of dispersal of spores of* Tilletia caries, 28 *July* 1933, *Exp.* 1

	Quantity of spores per cover-glass 18 × 18 mm. (average of two)			
Angle to wind	At 5 m. from place of dispersal of spores	At 10 m. from place of dispersal of spores	At 15 m. from place of dispersal of spores	At 20 m. from place of dispersal of spores
−20°	204	23	4	0
−10°	435	45	19	8
+30°	964	212	207	49
+45°	1198	587	87	142
+55°	659	123	77	15
+65°	341	24	26	7
+75°	365	5	26	53
+85°	20	10	9	14

Exp. 2 (5 September 1933) was conducted in the same place as the previous experiment. A mixture of spores of *Tilletia caries* and *Bovista plumbea* was disseminated through a small sieve at a height of about 1·5 m. Scattering of the spores took 15 min., after which 30–35 min. were allowed

(perhaps unnecessarily) to elapse for the deposition of the spores. The wind varied from 2·3 to 3·0 m.sec. and was sometimes calm. As shown in Table 5, three slides were placed at each trapping locus. Approximately $1{\cdot}8 \times 10^9$ spores of *Tilletia* were used but those of *Bovista* were unfortunately not estimated.

Stepanov's results led him to an empirical law of spore dispersal given as $y = C + a/sx$, where y = the distance at which the spores were trapped,

Table 5. *Dispersal of mixed spores of* Tilletia caries *and* Bovista plumbea, 5 *September* 1933. *Exp.* 2

Quantity of spores per cover-glass 18 × 18 mm. (average of three)

	Tilletia				*Bovista*			
Angle	5 m.	10 m.	20 m.	40 m.	5 m.	10 m.	20 m.	40 m.
−45°	3·0	0·3	0·7	0·0	0·3	0·0	0·0	0·0
−30°	128·0	2·3	0·3	0·0	7·0	0·3	0·0	0·0
−15°	43·3	54·7	4·7	0·3	7·0	4·0	0·0	0·0
0°	206·0	204·0	5·3	8·3	17·0	0·0	1·7	0·0
+15°	623·0	115·3	31·3	1·3	46·0	16·0	0·7	0·0
+30°	877·7	216·7	49·0	7·0	81·3	20·3	6·3	0·0
+45°	911·7	89·7	207·0	9·3	70·0	10·7	7·3	2·7
+60°	245·7	48·0	3·0	2·3	27·7	17·3	0·7	0·0

Table 6. *Calculation of parameters for Sutton's diffusion equation from Stepanov's data* (1935)

Exp. no.			Distance in m. 5	10	15	20	40
1	*Tilletia*	σ	2·25	2·97	5·03	6·64	—
		log σ	0·3522	0·4728	0·7016	0·8222	—
2	*Tilletia*	σ	1·81	3·62	—	4·87	14·79
		log σ	0·2577	0·5587	—	0·6875	1·1699
2	*Bovista*	σ	1·790	3·673	—	5·343	—
		log σ	0·2529	0·5651	—	0·7277	—
	log distance (m.)		0·6990	1·0000	1·1761	1·3010	1·6021

Equation for regression line:

$a = 0{\cdot}5971$ (S.D. 0·02), $b = 0{\cdot}8812$ (S.D. 0·072), $Y = 0{\cdot}5971 + 0{\cdot}8812\,(x - \bar{x})$.

Since $\sigma^2 = \frac{1}{2}C^2x^m$, $\log \sigma = \dfrac{2 \log C - \log 2}{2} + \dfrac{m}{2} \log x$,

whence $C = 0{\cdot}637$, $m = 1{\cdot}76$.

x = the number of spores deposited per unit area of trap surface, and C and a are parameters dependent on the conditions of the experiment; s = area of trap surface. The number of spores deposited is thus regarded as varying inversely as the first power of the distance from an origin. It will be shown later that Stepanov's formula, which represents the first experimental approach to the problem, needs modification if it is to describe spore dispersal over a wide range of conditions. First it will be necessary to re-examine Stepanov's data in the light of present knowledge of eddy diffusion.

The observed data enable us to test whether the standard deviation σ, of the spores from their mean position, agrees with Sutton's form: $\sigma^2 = \frac{1}{2}C^2x^m$, or with the older diffusion theories where $\sigma^2 = 4Kt$. The data also enable estimates to be made of the parameters m and C which can be compared with values obtained by previous workers for similar conditions. Examination of the data in Tables 4 and 5 shows that the spores at any one distance do not lie in a smooth normal distribution but are significantly clumped. This is probably due to the short time of the dispersal being insufficient to smooth out the action of a few large-scale eddies. The standard deviations of spores lying at each distance from the source have been calculated in Table 6, where for convenience the deviations from the

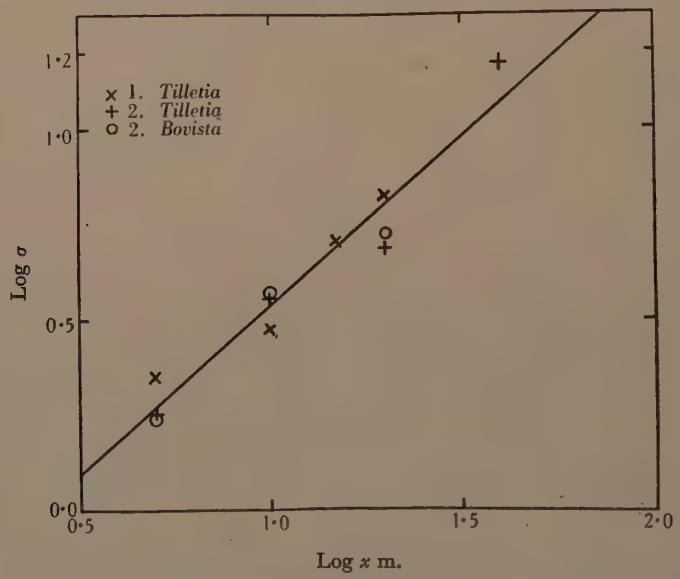

Fig. 2. Stepanov's experiments on liberating spores from a point. Relation between standard deviation of spores deposited at each distance from their mean position, and the distance from source. Also linear regression calculated from data showing agreement with Sutton's eddy diffusion theory where $\sigma^2 = \frac{1}{2}C^2x^m$ ($C = 0{\cdot}64$, $m = 1{\cdot}76$).

mean position at each distance have been measured along the arc with the point source as centre. The standard deviation at each distance has been calculated by the usual formula, $\sigma = \sqrt{[(x-\bar{x})^2/(n-1)]}$. This is not strictly legitimate, since the trapped spores are a systematic instead of a random sample of the population, and should be regarded as estimates of the ordinate of a normal frequency curve. However, the formula clearly gives a useful approximation, which would have been better if traps had extended farther laterally and if data for some of the intermediate radii had not been missing.

Both experiments were carried out in the same place, and with comparable wind velocities, and when values for log σ are plotted against log x, as in Fig. 2, it is found that the points lie reasonably close to a

straight line. The slope of this line is not unity, as it would have been with the older diffusion theories, but corresponds with Sutton's formula for σ, with $C = 0{\cdot}64$ and $m = 1{\cdot}76$. These values agree well with those found by other workers (Table 3), and especially for the exactly comparable data due to Richardson for dispersal of smoke from a point source over distances of tens of metres where $C = 0{\cdot}6$ and $m = 1{\cdot}75$. Sutton's work was apparently unknown to Stepanov when these experiments were carried out, and so the data could not at the time be analysed in terms of eddy diffusion. However, the good agreement between experiment and theory provides strong evidence that spore dispersal in air is mainly controlled by eddy diffusion of the type postulated by Sutton.

Stepanov's cross-wind data have been used to calculate the parameters C and m of the diffusion equation. We can now make independent use of his down-wind data to find out whether the numbers of spores deposited at each distance correspond with the numbers expected from Sutton's density formulae. To do this we shall have to adapt Sutton's formulae to the conditions of the problem, and it will be necessary to find a relation between the concentration of spores in a cloud and the number of spores deposited on a surface over which the cloud travels.

We have to trace the diffusion of a cloud of spores from a point source. It is not possible to assume that a steady state has been set up and that all traps are down wind. For fungus-spore data it is convenient to regard the total quantity of spores liberated, Q, as made up of a large number of small puffs which may or may not take the same direction, but which are all diffused in travel according to the relation $\sigma^2 = \frac{1}{2}C^2x^m$. Accordingly we choose Sutton's formula for an instantaneous point source

$$\chi = \frac{Q}{\pi^{\frac{1}{2}}C^3x^{\frac{3}{2}m}} \exp\left\{-\frac{r^2}{C^2x^m}\right\}.$$

The cloud travels down-wind, and in these experiments its centre is initially at a height z of about 1–1·5 m. above ground level. Except at distances near to the source this will not affect the argument much, and it has in fact been neglected throughout. The surface of the ground is regarded as cutting through the centre of the cloud so that the cloud is not free to expand downwards, and consequently the concentration above the xOy plane will be approximately double what it would have been in the free air. We can represent this by writing $2Q$ in place of Q in the formula. This treatment differs from that of Schmidt, who assumed that any spore which had been calculated to have diffused to the ground level would have been deposited, the ground thus apparently acting as a sieve. In our theory the ground is more appropriately regarded as reflecting the cloud. Any point on the x-axis (at height $z = 0$) will be exposed during the passage of the cloud over it to a succession of volumes of air varying in spore content from an initial zero, up to the maximum of $\chi = \dfrac{2Q}{\pi^{\frac{1}{2}}C^3x^{\frac{3}{2}m}}$ at the centre of the cloud, and down to zero again. If we imagine a ring around the point source, with radius x, and 1 sq.cm. cross-section, the total number of spores passing through the ring during the passage of

the cloud will be the same as the number in a slice through the cloud in the xOy plane 1 cm. thick. Following Sutton's assumption that the lateral and vertical spread of the cloud is small compared with the distance of travel, and that consequently the density of spores in the cloud remains unchanged during the passage of the cloud across the ring, it can be shown (see Appendix) that the total number of spores, $\mathcal{N}$, flowing through the ring is given by $\mathcal{N} = \frac{2Q}{\sqrt{(\pi)}\, Cx^{\frac{1}{2}m}}$. The mean number, n, passing across 1 c.cm. at the distance x is given by $n = \frac{\mathcal{N}}{2\pi x}$ or $n = \frac{2Q}{2\pi^{\frac{1}{2}} Cx^{\frac{1}{2}(m+2)}}$. As under any given set of conditions the number of spores deposited from 1 c.c. of air is likely to depend only on the number of spores in that volume of air, we should expect the total deposition, D, on the surface under the ring to be a constant fraction of $\mathcal{N}$, say $D = p\mathcal{N}$, and similarly d, the mean deposition per sq.cm. on the ring would be $d = pn$. The number p, which will be referred to as the deposition coefficient, answers the question: if n spores per c.c. flow across 1 sq.cm. of surface, what number will be deposited on the surface? Obviously it is a number of considerable biological importance, for

Table 7. *Number of spores deposited per total trap surface of* 25·92 *sq.cm. at various distances from the point source in Stepanov's experiments*

Exp. no.	Spores of	No. liberated Q_0	Distance in m. 5	10	15	20	40
1	*Tilletia*	$1{\cdot}2 \times 10^9$	4186	1029	455	288	—
2	*Tilletia*	$1{\cdot}8 \times 10^9$	3038·4	731·0	—	301·3	28·5
2	*Bovista*	Unknown	256·3	68·6	—	16·7	2·7

instance, in pollination, as well as in epidemics and their control by protective dusts. Under stream-line conditions p could, of course, be calculated as the resultant of wind speed and the terminal velocity of the particle, as attempted by earlier writers, but little can yet be said about the factors affecting its magnitude under turbulent conditions, and the matter awaits empirical investigation in the field and possibly by wind-tunnel tests where deposition could be studied without progressive dilution of the cloud. Measurements correlating air content and spore deposition are lacking at present. Meanwhile p must be derived from the data empirically.

In Table 7 are shown the sums of the numbers of spores deposited in Stepanov's experiments at all angles to the prevailing wind for each distance from the source. From the values of Q_0 given for experiments with *Tilletia*, and assuming provisionally that there was no diminution of the number of spores in the cloud through deposition, a preliminary calculation shows that the mean number of spores flowing over 1 sq.cm. of a ring on the axial plane of the cloud at a distance of 5 m. would be $n = 6{\cdot}32 \times 10^3$ in Exp. 1, and $9{\cdot}5 \times 10^3$ in Exp. 2. Stepanov's traps at each distance had a total area of 25·92 sq.cm. Actually the traps only sampled a sector of 105° out of a possible 360°, and some few spores were trapped

at most positions on even the most extreme radii, but it is probable that if the traps had been continued round the full circle few more spores would have been caught. Dividing the observed deposition on all the traps at any one distance by 25·92 will give an approximate value for d. With *Tilletia* at 5 m. this operation gives $d = 161{\cdot}5$ for Exp. 1, and $d = 117{\cdot}2$ for Exp. 2. Since $d = pn$, we can now make a preliminary estimate of the deposition coefficient as $p = 0{\cdot}026$ and $0{\cdot}012$ respectively in the two experiments.

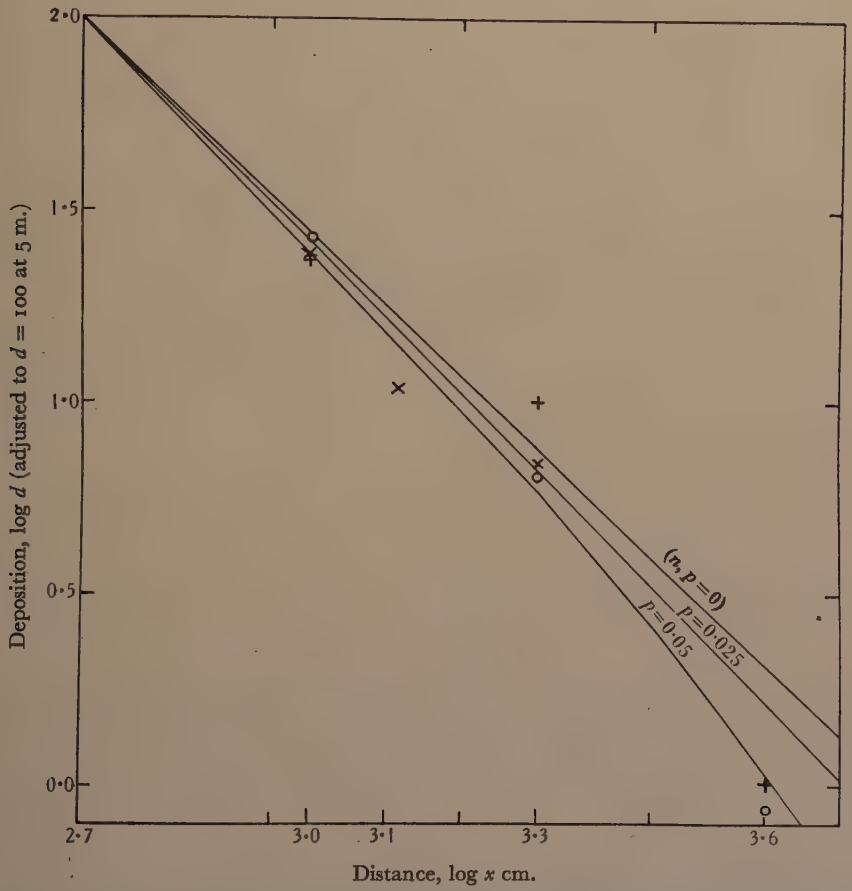

Fig. 3. Stepanov's experiments on liberating spores from a point. Relative numbers of spores deposited, and distance from source (all directions pooled, and each series adjusted to density of 100 at 5 m.). Also curves showing d expected with two trial values of the deposition coefficient, p and n for $p = 0$.

Sutton's formulae were developed for calculating the densities in a cloud of particles whose deposition was negligible, the number of particles in the cloud, Q, remaining constant throughout the diffusion. In our problem, although the effect of gravity on dispersal has been shown to be small and has been neglected, the quantity of spores is steadily diminishing

owing to a relatively large deposition from that part of the cloud in contact with the ground, so that Q_x, the total quantity remaining in the cloud when its centre has moved a distance x, is less than the original Q_0. It can be shown (see Appendix) that Q will decrease exponentially with increasing distance according to the equation

$$Q_x = Q_0 \exp\left[-\frac{2px^{(1-\frac{1}{2}m)}}{\sqrt{(\pi)}\,C(1-\frac{1}{2}m)}\right].$$

Values of Q_x and d for two values of the parameter m have been computed (see Appendix, Table 21).

It is now possible to test the theory against Stepanov's data. In each of his experiments the original number of spores liberated differed, so the data must first be put on a comparable basis by equating the mean deposition, d, at 5 m. to 100%, and then expressing the deposition observed at greater distances by relative percentages. In Fig. 3 the logarithms of the observed relative depositions are plotted against the logarithms of the distances in centimetres. The expected depositions when $p=0{\cdot}05$, $0{\cdot}025$ and zero respectively are also plotted. As p decreases the slope of the line of expected densities also decreases, and approaches the limiting value of $\frac{1}{2}(m+2)$. It will be seen from Fig. 3 that the line calculated for $p=0{\cdot}05$ approaches most closely to the observed values. An increase over the provisional value for p obtained in the preliminary calculation, when Q was assumed to remain undiminished by deposition, was to be expected, as Table 21 shows that about a quarter of the spores liberated would probably have been deposited by the time the cloud reached a distance of 5 m. A deposition coefficient of $p=0{\cdot}05$ means that in travelling across 1 sq.cm. of surface the entire cloud would deposit a quantity of spores approximately equivalent to the number contained in a slice half a millimetre thick through the axial plane of the cloud xOy. Mean values for wind velocity during the experiments were not given, but from the data would probably not be less than 1 m.sec. At this speed of travel 0·5 mm. of cloud would be cleared in about 1/100 sec., the time taken to travel a distance of 1 cm. This represents about five times the thickness of the cloud that would be expected from the known terminal velocity of fall of spores of *Tilletia* in still air, and may indicate that particles are deposited more rapidly from turbulent than from still air.

IV. Plant-disease gradients

Stepanov's experiments give evidence that Sutton's eddy diffusion theory is applicable to the dispersal and deposition of dry fungus spores in air under average day conditions from a point source, provided that the diminution of the number of particles in the cloud through deposition is taken into account. No other available experiment allows the various parameters for the field to be estimated, but in plant disease literature there are records giving quantitative data on the numbers of spores, lesions, infected individuals, etc., observed at different distances from the presumed source of the disease. Before the deposition formulae can be

applied to plant-disease gradients there are several difficulties to be considered.

Meteorologists have been interested principally in diffusion during short periods of time of the order of 10–100 min. during which the wind can usually be considered to have a mean direction and velocity. Biological data often refer to sampling periods of days or even months, during which the wind undergoes major changes in direction and velocity. Changes in wind velocity, without changes in the direction, are, however, on Sutton's theory relatively unimportant. Since $\sigma^2 = \frac{1}{2}C^2x^m$, the density of the cloud depends on the distance travelled by the cloud and not on the time taken to travel that distance. Changes in wind direction, however, introduce a factor which cannot be dismissed so easily. Two special cases can be considered here. When records are available in all directions around a symmetrical source the mean deposition per sq.cm. irrespective of direction is given by d. If dispersal has taken place while the wind came from a uniform direction, as may happen when conditions for the spread of a disease are favourable for periods of only an hour or two as with potato Late Blight, then if observations are made only at points down-wind the relative deposition will be given by d_w (Table 21). This down-wind deposition gradient is very similar to d, but slightly flatter under normal conditions and steeper under low turbulence conditions.

The deposition equation gives the number of particles expected when the parameters Q, m, C and p are known. Measurements of these have not been made so far in connexion with any plant disease, and it will be necessary to assume values for average conditions of the atmosphere found by other methods. Also, since the strength of the source of infection varies greatly from field to field, the equation will give only the relative numbers of spores deposited at each position. This number is probably always many times greater than the number of spores which are successful in infecting plants and causing lesions, and must vary greatly under different conditions. The proportion should be uniform, however, over the imaginary uniform field which we postulate. All these factors influence the height of the curve above the x-axis but do not affect its shape.

When disease data are given as the number or percentage of plants attacked irrespective of whether the plant has one or many lesions, aphid punctures, etc., the percentage will have to be suitably transformed before the formula for deposition can be applied. The method used was worked out by Thompson (1924) who gave a table from which the necessary correction can be made. The conversion, which becomes necessary only when the proportion of infected individuals is above about 20%, will be referred to as Thompson's transformation. It depends on the fact that if in a group of say 100 individuals there is only one lesion, then obviously only one individual, or 1%, can be infected. A second lesion occurring at random on the same group of 100 individuals will have one chance in 100 of infecting the individual that already has one lesion, and so on. It can be shown that to infect 50% of the individuals in a large population it would take about seventy randomly distributed lesions per 100 individuals. Conversely, the table can be used to detect non-random distribution, due

to such factors as leaves in different positions on a plant not being equally suitable environments.

Stakman (1942) rightly stresses the need for experiments with 'marked' spores or pollen grains, easily identifiable and of known origin, in order to facilitate the development of the principles of aerobiology. Many spores are of almost ubiquitous occurrence in the air, and it is impossible to know from whence they come. This fact raises the question in interpreting field data of whether a significant proportion of the spores trapped, or lesions counted, represent contaminations from sources other than the one under consideration. The effect of any general contamination will consist of a uniform addition to the observed deposition at all distances from the particular source under investigation. The effect of this addition will be to flatten the gradient so that, plotted on a log-log scale, the line would ultimately become parallel to the x-axis. Most of the data from field observations which are quoted below do not show such an effect, but one or two examples are given.

The basidiospores of rusts and the sporangia of downy mildews are known to be relatively short-lived when dry, but there seems to be no evidence that death of spores in transit would decrease the number of successful infections over the distances of tens or hundreds of metres discussed in this paper. In a wind as slow as 0·5 m.sec. the sporidia of *Cronartium ribicola* would take only about 10 min. to travel the 900 ft. regarded as the normal limit for infection of pines by this fungus. From data on the viability of its sporidia given by Spaulding and Rathbun-Gravatt (1926) the absence of disease on plants at 900 ft. seems more likely to be due to the great dilution of the cloud, making infection very improbable.

Field observations are complicated by the fact that sometimes records were not made until after lesions derived from the original source had themselves multiplied and acted as new sources for the spread of the disease. As far as possible, such complications have been avoided in the examples chosen below. The effect would be to flatten the observed gradient, because we should have to deal not only with the original source, but also superimposed on this the effects of a series of contaminations varying according to the distance from the original source. Such cases cannot be dealt with systematically at present.

The deposition formula can now be compared with data from published papers on plant-disease gradients, where the numbers of spores, lesions or diseased plants have been counted at various distances from a source of disease. Many published observations have had to be excluded because one or more essential measurements are not clearly given. References to disease gradients are frequent but quantitative studies are very rare, though no doubt many sets of data have been overlooked in the present survey. It should be pointed out that observations have been gathered by the workers concerned as part of routine studies and without any reference to a possible general study of gradients. This adds interest to the following collection of data, most of which agree reasonably well with the deposition expected from the eddy diffusion theory, but one or two of which show marked divergences.

In the following examples the data are plotted in Figs. 4 and 5 on a log-log scale. On the y-axis is plotted $\log_{10}$ observed number of spores or lesions, and on the x-axis is plotted $\log_{10}$ of distance from the source in centimetres. For comparison two theoretical lines are also plotted for the appropriate formula, one is for ordinary turbulent conditions with $m = 1{\cdot}75$, and one for very low turbulence with $m = 1{\cdot}24$. Q_0 for these theoretical lines is chosen as 10^{10} in Fig. 4, which is a number of spores of the order that might be encountered in the field. (Christensen (1942) found that an acre of wheat moderately affected with *Puccinia graminis* would produce at least 10^{11} spores, and Buller (1922) estimated that one

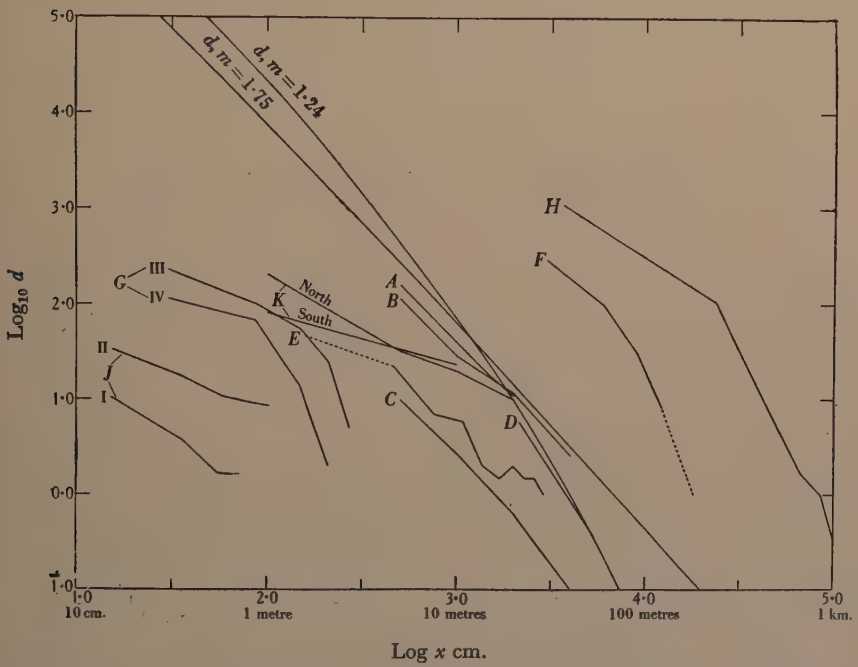

Fig. 4. Observed plant disease gradients from a point source, plotted on double log scale. Also lines showing expected values for normal and low turbulence conditions ($m = 1{\cdot}75$ and $1{\cdot}24$ respectively) calculated for $Q_0 = 10^{10}$ spores. *A* and *B*, *Tilletia caries* spores, Stepanov; *C*, *Bovista* spores Stepanov; *D*, *Puccinia coronifera* spots on oats, Grushevoi; *E*, *Cronartium ribicola* cankers on pine, Buchanan and Kimmey; *F*, *Phytophthora infestans*, Bonde and Schultz, on potato; *G*, *P. infestans* on potato, Limasset; *H*, *Peronospora destructor* on onions, Newhall; *J*, *Botrytis tulipae* on tulip, Wallace; *K*, *Cercosporella herpotrichoides* on wheat, Oort.

puff-ball, *Calvatia gigantea*, produced 7×10^{12} spores.) To atone for our previous arbitrary treatment of the deposition coefficient, due to lack of experimental data, the value for p found in Stepanov's experiments has been adhered to throughout and so has the value for C. Subsequent work should throw more light on the variability of these parameters.

When field data for passively air-borne spores are plotted on the same graph the slope of the line at any distance should not normally be less

than the slope of the theoretical line for $m = 1{\cdot}75$ at the same distance. With organisms which liberate their spores and initiate infection under very humid conditions of fog, or in the early morning hours when diurnal turbulence is at a minimum, such as potato blight (*Phytophthora infestans*), the observed gradient might be expected to approach the theoretical curve for low turbulence where $m = 1{\cdot}24$.

(1) *Gradients from a point source.* Data on the dispersal of spores of *Tilletia caries* and *Bovista plumbea* obtained by Stepanov (1935) have already been described in detail. All three series (Fig. 4 *A*, *B* and *C*) agree reasonably well with the slope of the theoretical line for normal turbulence. In *Tilletia caries* the lines are lower than the theoretical line, which was calculated for $Q_0 = 10^{10}$, by an amount proportional to the strength of the source (Exp. 1, $Q_0 = 0{\cdot}12 \times 10^{10}$ and Exp. 2, $Q_0 = 0{\cdot}18 \times 10^{10}$).

Table 8. *Crown rust* (Puccinia coronata) *on oats near a* Rhamnus *bush*

Mean number of lesions per plant (Grushevoi, 1929, cited from Stepanov, 1935)

Distance from buckthorn bush	3 July Mean no. lesions per plant	13 July Mean no. lesions per plant
'Directly neighbouring'	10·38	24·38
10 sazhen (70 ft.)	5·70	19·09
25 sazhen (175 ft.)	0·35	6·85

A gradient of infection of oats with crown rust (*Puccinia coronata*) in proportion to the distance from an infected bush of *Rhamnus*, the alternate host, was described by Grushevoi (cited from Stepanov, 1935: see Table 8). Two points only are available for plotting, as the nearest of the three samples was merely stated to be 'directly neighbouring' the buckthorn bush. Counts were made on two dates. The count made on 3 July when the plants were in the flowering stage agrees well with the gradient expected for average conditions (Fig. 4 *D*). Ten days later another set of counts was made and a flatter gradient observed, presumably owing to the secondary spread of the disease.

Blister rust (*Cronartium ribicola*) is perennial in the stems of five-needled pines. On this host it produces aecidiospores which are capable of infecting only the leaves of the currant (*Ribes* sp.). On the currant are produced uredospores capable of infecting other currants, and also teleutospores which on germination produce the sporidia (basidiospores) which are able to infect only pine needles. Spaulding (1920) noted a regularity about the gradient of infection on *Pinus strobus* observed by Prof. Pennington in the Adirondacks: 'In general, it may be said that under given conditions the number of infections in pine varies directly with the amount of *Ribes* leaf surface, and inversely as the square of the distance from *Ribes*.' Blister rust gradients were studied experimentally on *Pinus monticola* in British Columbia by Buchanan and Kimmey (1938). Blocks of uninfected pine, 22·5 acres in area, were cleared of all currant bushes except for a group at the centre of the plots. These currants were inoculated to serve as a source of infection. *Ribes* was also removed from various zones around the plots. The infections on the pines resulting from spores produced by

diseased currants were sometimes distributed evenly in all directions, but when the plots were on slopes the lesions tended to be more numerous down the slopes. Some of Buchanan and Kimmey's tables show marked gradients, but as data are expressed in units of 'trees' of very diverse size they are not suitable for our purpose. From one of their graphs, however, can be read the pooled results of all their experiments in terms of cankers per million leaves, and the data are given in Table 9. When plotted (Fig. 4 *E*) the gradient shows a general agreement with the expected distribution, but also illustrates one or two points of discrepancy. The first point plotted on the graph is entered at 5 ft., which is the mean of the first zone measured from the plot centre, but as this central zone differs from all other zones in being partly occupied by the *Ribes* source instead

Table 9. *Average number of cankers of* Cronartium ribicola *per million* Pinus *leaves exposed in* 10 *ft. zones out from central* Ribes. (Buchanan and Kimmey, 1938. Data for all plots combined)

Distance from plot centre (ft.)	No. cankers per million leaves
0–10	46·5
10–20	22·5
20–30	7·0
30–40	6·0
40–50	2·0
50–60	1·5
60–70	2·0
70–80	1·5
80–90	1·5
90–100	1·0
100–110	2·0

of pine trees it is not surprising that the number of cankers recorded should be lower than the theoretical value. The second point of interest is that beyond about 60 ft. the number of lesions becomes practically constant, suggesting that in some of the plots which contribute to the data a contamination on a low level may have been coming in from outside. A similar effect from a contamination was observed by Brunt (1932) for smoke pollution around the City of Norwich.

Gradients for a disease with a similar life cycle were given by Schneiderhahn (1926) in studies on cedar rust of apples (*Gymnosporangium juniperi-virginianae*), but unfortunately they cannot be used because information on the magnitude of the source is lacking.

Gradients of two sets of data of infection due to potato Blight (*Phytophthora infestans*) are available, but neither is well suited to our purpose. One of great interest is that of Bonde and Schultz (1943), who traced blight developing in potato fields in Maine to its origin in waste potato dumps of the previous year's crop. One of their tables gives the number of lesions at specified distances from one such dump which we can treat as approximating to a point source. The counts were presumably taken down wind in the direction of greatest spread, though this is not definitely stated. Their table gives both the percentage of plants infected and the number of lesions per 100 plants. Applying Thompson's trans-

formation to the percentage figures we find that the observed numbers of lesions are of the same order as would be expected if their distribution at each distance were random, and so it can be concluded that the lesions observed do in fact represent infections coming from the primary focus and that the position is not complicated by local spread from a second generation of spores (Table 10). The first point of the curve (Fig. 4 *F*) is unexpectedly low, perhaps owing to the difficulty of finding as many as 100 plants at exactly 100 ft. from a point source, but the remainder of the gradient is compatible with dispersal under low turbulence conditions.

Table 10. Phytophthora infestans. *Late blight in potato field near infected refuse pile in Maine* (Bonde and Schultz, 1943)

Distance from refuse pile ft.	Plants infected % (observed)	Lesions per 100 plants (observed)	Lesion no. expected from Thompson's transformation
100	98	293	395
200	55	98	80
300	21	31	24
400	6	9	—
500	0	0	—
600	1	2	—

Table 11. *Potato plants infected with* Phytophthora infestans *near primary foci on 31 July* (Limasset, 1939)

Mean distance from edge of infector group cm.	No. infected total plants	Percentage infected *y*	Probable lesion no.
	Focus III		
30	19/28	68	114
90	15/32	46·8	63
150	6/44	13·6	14
210	1/50	2·0	2
	Focus IV		
30	25/28	89	221
90	20/32	62·5	97
150	19/44	43	53
210	11/50	22	25
270	3/60	5	5

The fluctuation at 400–600 ft. illustrates the importance of increasing the size of the sample when the number of lesions is low.

Another set of data on *Phytophthora infestans* comes from Limasset (1939), who investigated the role of diseased potato seed tubers in forming primary foci when planted in a crop. Compact groups each of twenty infected tubers of the variety Early Rose were planted in a plot of the variety Saucisse to act as a source of the disease. On 28 July, after a rainy period, blight appeared on some of the shoots emerging from infected tubers, but at that time the disease was not seen elsewhere in the district. The disease spread to surrounding plants, and from the data given and a plan of the field, scale diagrams have been made from which Table 11 was prepared. The shape of the source in these experiments was approximately

a circle of 200 cm. radius, and the effect of the disk source has obviously been to flatten the gradient (Fig. 4 *G*), especially at points near to the source; so to regard this as a point source can only be a very rough approximation. However, the agreement in general trend of the gradients on the two plots is worth noting.

Downy mildew on onions (*Peronospora destructor*) was studied by Newhall (1938) in Wayne County, N.Y. The source consisted of a tenth of an acre of onion bulbs grown for seed in the north-west corner of a valley (a similar source lay a quarter of a mile back). Counts were made of the number of lesions on different onion fields, grown for the bulbs, at various distances from the source down the valley. It will be appropriate to treat the source as a point in relation to most of the fields, though the nearest readings might be expected to show the effect of the area of the source (see following section). The dispersal is not over a uniform field but refers to a number of fields in which conditions may be expected to differ considerably. The data given in Table 12, when plotted (Fig. 4 *H*), give a gradient suggesting dispersal under low turbulence conditions.

Table 12. *Dispersal of onion downy mildew lesions from a point source* (Newhall, 1938)

Distance from source (ft.)	No. of lesions per 100 ft. row
120	1135
780	107
1750	4
2200	1·7
2800	1·0
3300	0·33

In the two cases to be described next the data are not compatible with the scattering expected by eddy diffusion. They are gradients of infection with *Botrytis Tulipae* and *Cercosporella herpotrichoides*.

Wallace (1934) studied the distribution of secondary leaf spots on beds of tulips (William Copland) growing out of doors in Lincolnshire, and gave diagrams showing the number of spots on plants situated near a tulip shoot bearing spores of *Botrytis Tulipae*. In a letter, Mr E. R. Wallace states that the bulbs were planted about 5 in. apart in rows 7 in. apart, with a path of 18 in. between the beds, and from a scale diagram Table 13 was prepared. On plotting the log number of lesions per plant against the log distance in centimetres, we obtain gradients (Fig. 4 *J*) quite incompatible with the eddy diffusion theory. The minimum possible slope (even under very low turbulence and with no diminution in Q_0 through deposition) would be $\frac{1}{2}(m+2) = 1{\cdot}62$, whereas the first bed has a gradient of about 1·3 and the second as low as 1·0. Beaumont, Dillon Weston and Wallace (1936) state that *Botrytis Tulipae* is dispersed in the field by two methods, wind and splashing in rain drops. It is suggested in explanation of the anomalous gradients that they are examples of splash dispersal and not of wind transfer. Examination of the weather records kept at the Kirton Agricultural Institute where the crop was growing supports this

explanation. Disease records were made during a dry period, but in each case over a tenth of an inch of rain fell 5 days prior to making the counts. The rainfall records were: 20–30 March, nil; 31 March, 0·12 in.; 1 April, nil; 2 April, 0·1 in.; 3–8 April, nil; 9 April 0·13 in.; 10–17 April, nil. (These records are published by kind permission of the Principal of the Kirton Agricultural Institute.) Unfortunately, nothing is known about

Table 13. *Distribution of spots on tulip plants near to shoot-bearing conidia of* Botrytis Tulipae (Wallace, 1934)

Mean distance from focus (cm.)	Mean no. lesions per plant
First bed (focus removed and spots counted 4 April 1933)	
15·2	10·5
35·8	3·72
54·4	1·67
Second bed (spots counted 13 April 1933)	
15·3	33·4
34·6	17·9
58·0	10·7
79·8	9·48
102·0	8·70

Table 14. *Influence of the distance from the source of infection on the occurrence of* Cercosporella herpotrichoides

Distance from source of infection m.	Percentage culms with eyespots	Probable no. of lesions (Thompson's transformation)
	To north	
1	87	205
5	28	35
10	18	20
20	10	10
35	8	8
50	11	11
60	11	11
70	1	1
	To south	
1	56	82
10	26	30

the type of gradient given by splash-dispersed spores, but it is worth noting that the gradients given by this *Botrytis* are similar to that found in the undoubted case of splash dispersal that follows.

The spread of Eye-spot of wheat (*Cercosporella herpotrichoides*) was studied by Oort (1936). In the middle of a field of autumn-sown wheat, where the disease had not previously appeared, twenty plants badly attacked by the fungus were transplanted to a small patch in December 1934. In the following July samples of about 200 culms each were collected at different distances from the diseased patch and inspected for Eye-spot with results given in Table 14. When plotted (Fig. 4 *K*) the gradient obtained is totally incompatible with the eddy-diffusion theory (still more so after

applying Thompson's transformation). There is a suggestion in Oort's data that in addition to the lesions derived from the source, there may have been some infections due to a general contamination from the same or neighbouring fields. Over the experimental field itself, Oort recorded the presence of small secondary infections high up the culm, and stated that only within about 10 m. of the artificial source were infections to be found at the foot of the culm. The figures show no obvious decrease after 10 m., but only what are probably fluctuations due to sampling, so the possibility is that there is a contamination averaging about 8% not due to the source. When plotted the gradient, which mainly represents the effect of the artificial source, is flatter than demanded by the eddy-diffusion theory. This is of interest when taken in connexion with the findings of Sprague and Fellows (1934), who state that Eye-spot increases suddenly in the north-western United States after heavy rains in spring; that spores are carried by splashing water; but that there is some evidence that spores are sometimes air-borne. So that, although Mason (1937) puts *Cercosporella* among the dry-spored fungi, the evidence is that this species is normally dispersed by water, and it is therefore not surprising that the eddy diffusion formulae should not apply. Alternatively, it is possible that the original gradient has been flattened by local secondary infections.

(2) *Gradients from a line source.* The deposition formula so far used is appropriate for particles scattered from a point source. With many sets of data, however, the source is significantly long, or both long and wide. It would then be appropriate to use a formula derived by integrating the effect of all sources over the line or area from which the particles are being dispersed. Such an integration cannot conveniently be dealt with. When more data are available on the various parameters of the diffusion equation it will probably be worth while to carry out mechanical integration for sources and samples of standard dimensions and for standard sets of conditions, but for the present only an approximation can be attempted. This can be done by integrating the effect of an infinite line source Oy, liberating Q_0 spores per cm. while the wind is blowing in the direction Ox. The deposition per sq.cm. at a distance x cm. down wind from an infinite line source is then given approximately by

$$d_{lw} = \frac{p\,2Q_x}{\sqrt{(\pi)}\,Cx^{\frac{1}{2}m}} \quad \text{(see Appendix, Table 21).}$$

Sutton observed that a finite line source appears to behave as an infinite line source for distances up to four times its length (this is because the lateral effect of parts of the source which are not up-wind is very small), so this approximation would be appropriate where the source is a crop row, a hedge, or a weed strip on a headland, etc. At any point the major contribution to the deposition would be expected to be that carried by winds which were directed along the x-axis. Little more can be said in justification of the approximation except that in practice the gradients from line sources described in the next few examples are flatter than would

be expected from a point source, and approach the curve expected from this formula.

At points very close to the source its width will have to be taken into account. It will be evident that deposition from a strip will fall off less rapidly than from a line source, just as deposition from a line source falls off less rapidly than from a point. Further, while a 10-acre field ought to be treated as a strip source for points in adjoining fields, for fields a few miles away it would be appropriate to choose the formula for a point source.

The first gradient from a line source to be described is unusually steep; it refers to trapping of aecidiospores of *Puccinia graminis*. Lambert (1929) quotes some observations of Christensen at Northfield, Minnesota, where a barberry hedge, consisting of 175 heavily infected bushes, most of them 6 ft. or more high, was found on a deserted farmstead. The total production of aecidiospores from the hedge was conservatively estimated at over 1000×10^{10}. Vaselined glass slides were exposed vertically 3 ft. above the ground on 24–25 May 1932, for a period of 20 hr. during a period when spores were being liberated at a tremendous rate. The numbers of spores trapped at different distances from the hedge are shown in Table 15.

Table 15. *Numbers of aecidiospores of* Puccinia graminis *trapped near a barberry hedge* (Lambert, 1929)

Distance from barberry hedge ft.	No. of spores trapped per slide 3 × 1 in.
3	160,000
6	33,000
23	210

Other slides were exposed on other dates and for different lengths of time, and some spores were trapped up to a mile from the bushes. Plotted on a log-log scale this decrease in deposition represents an exceptionally steep gradient (Fig. 5 *A*), not incompatible with the eddy-diffusion theory, but indicating either a higher value for the deposition coefficient, p, than that assumed hitherto, or that the traps were not down wind. Aecidiospores of *P. graminis* are discharged singly or in clumps to a distance of 4–5 mm. from the cup, and discharge takes place only in an approximately saturated atmosphere. Buller (1924), who studied the phenomenon, also reported the occasional discharge of what he called 'aecidiospore-bombs', or clumps containing 60–150 individual spores. The discharge of spore aggregates as well as single spores might explain an unusually high value for p.

The dispersal of aecidiospores of *P. graminis* from a barberry hedge was also studied by Johnson and Dickson (1919), but instead of trapping spores they counted infected stems of *Agropyron repens*. From their diagram the hedge seems to have been about 100 yd. long running north and south, and observations were made at distances up to 425 yd. from the hedge in a north-easterly direction. The line-source formula should therefore be reasonably appropriate for the data given (Table 16). The samples apparently consisted of 200 plants at each locus, and larger samples would

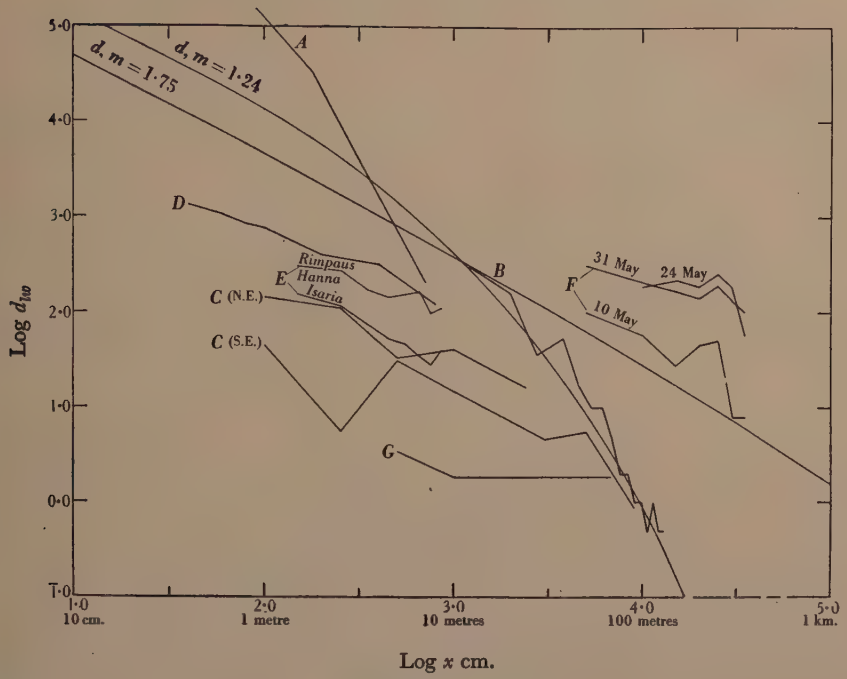

Fig. 5. Observed plant disease gradients from line and strip sources, plotted on double log scale. Also lines showing expected values for ordinary and low turbulence conditions, calculated for $Q_0 = 10^7$ spores. *A*, *Puccinia graminis* aecidiospores, Lambert; *B*, *P. graminis* spots on grass, Johnson and Dickson; *C* and *D*, *Tilletia caries* on wheat, Oort; *E* and *F*, *Erysiphe graminis* on barley, Pape and Rademacher; *G*, *Puccinia coronifera* on oats, Gassner.

Table 16. *Spread of* Puccinia graminis *to grass from rusted barberry hedge* (Johnson & Dickson, 1919)

Distance from barberry hedge ft.	Percentage grass stems infected	Probable no. of lesions by Thompson's transformation
15	100	—
40	95	300
65	80	165
90	30	36
125	41	54
150	15	17
175	10	—
200	10	—
225	5	—
250	2	—
275	2	—
300	1	—
325	1	—
350	0·5	—
375	1	—
400	0·5	—
425	0·5	—

have been required to obtain more accurate estimates of the percentage infection at the farthest distances. At 15 ft. 100% of the plants were infected, and so no estimate can be made of the number of spores successful in establishing lesions at that distance, but estimates can be made at distances of 40 ft. and upwards by applying Thompson's transformation. When plotted (Fig. 5 *B*) a steep gradient is obtained which is compatible with dispersal from a line source under low turbulence conditions.

Loose smut of wheat (*Ustilago Tritici*) was studied by Oort (1940) in connexion with the Dutch scheme for issuing health certificates for seed wheat, to find how far the health of a crop was affected by disease on neighbouring fields. In one experiment at Wageningen a rectangular strip of wheat which had been artificially heavily contaminated with loose smut

Table 17. *Spread of loose smut of wheat* (Ustilago tritici) *at Wageningen* (Oort, 1940)

Distance from strip source m.	No. smutted heads in sample of seed*
Direction north-east	
1	145
2·5	113
5	33
10	40·4
24	16·6
Direction south-east	
1	45
2·5	5·6
5	31·4
10	14·8
25	4·6
50	5·5
90	0·9

* Mean number of smutted heads per pair of plots of area 200 sq.m. from seed sampled at each distance.

was bounded on the north-east and south-east sides with smut-free wheat. At harvest time, samples were taken at different distances from the diseased rectangle in both north-east and south-east directions, and the seed was sown in the following season and the numbers of loose smut *heads* counted. In Table 17 is given the number of smutted heads for a sample area of 100 sq.m. This area would contain about 20,000 heads, and as the highest number of smutted heads recorded was only eighty-five, or less than 1%, it is clear that Thompson's transformation need not be applied. The question if smut-infected plants tiller as freely as healthy ones is also irrelevant since the numbers at the different distances are only relative.

Another experiment was carried out at Sprundel on a field situated at a great distance from other wheat fields. The field was sown with wheat which had been carefully treated with hot water, except for a small plot 10 m.sq. sown with seed of the same variety heavily infected with loose smut to serve as a source of infection for the rest of the field. This square had 1350 smutted heads in the summer of 1937. In August, samples were

harvested in different directions and distances from the contaminated square. These were planted in the following season. The numbers of smutted heads per 100 m. of plot grown from these samples is shown in Table 18 for distances from 0 to 8 m. in the north, south, east and west directions. (Data for other directions and distances are incomplete.) Both

Table 18. *Spread of loose smut of wheat* (Ustilago tritici) *at Sprundel* (Oort, 1940)

Distance from square source m.	Total smutted heads in sample plots of 400 sq.m. in all directions from source
0·4	1362
0·6	1082
0·8	857
1·0	769·9
1·2	507·9
2·0	403·5
4·0	319·4
8·0	121

Table 19. *Spread of* Erysiphe graminis *from winter to spring barley at Kitzeberg, Schleswig-Holstein* (Pape & Rademacher, 1934)

Distance from strip source (mean) m.	Percentage plants affected (mean of S.W., N.E., S.E. and N.W. directions)	Probable lesion no. (Thompson's transformation)
Variety *Isaria* (mean of four directions)		
1·5	79	156
2·5	69·5	119
3·5	52·5	75
4·5	41	53
5·5	36·2	47
6·5	30	36
7·5	26·2	30
8·5	32·2	40
Variety *Rimpaus Hanna* (mean of two directions)		
1·5	95·5	310
2·5	93·5	275
3·5	82·5	177
4·5	76·5	145
5·5	79·0	156
6·5	80·0	161
7·5	60·5	93
8·5	67·5	112

these experiments of Oort's give similar gradients (Fig. 5 *C*, *D*) which are compatible with diffusion down wind from a strip source under normal atmospheric conditions.

Gradients from strip sources were observed by Pape and Rademacher (1934) in studies on the spread of powdery mildew (*Erysiphe graminis*) from winter barley to adjacent spring-sown barley in Schleswig-Holstein. One at Kitzeberg, for which data are most complete, consisted of a plot of winter barley 7 × 13 m., surrounded by spring-sown barley. On the day after which mildew spots first appeared on the surrounding spring-sown

barley, the percentage of plants infected was counted at a series of distances from the edge of the plot in several directions. Results for two varieties given in Table 19 show a gradient (Fig. 5 *E*) flatter than would be expected from a point source, but compatible with diffusion by eddies from a strip. On some of the other gradients, studies were made late enough for secondary spread to have taken place; for these reference should be made to the original paper. One plot which was scored on a series of dates is of interest in showing the progressive damping out of the gradient following local secondary spread of infection (Table 20, Fig. 5 *F*). In several of their tables the authors gave both the percentage of plants attacked and the number of spots on leaves of different ages. Unfortunately, these data cannot be used to test the appropriateness of Thompson's transformation because the two sets of data were not derived from the same groups of plants.

Table 20. *Development of mildew* (Erysiphe graminis) *on field of spring barley at Screvenborn, Kiel, adjoining a field of winter barley* (Pape & Rademacher, 1934)

Distance from source m.	10 May Probable lesion no.	24 May Probable lesion no.	31 May Observed lesion no.
50	102	—	314·4
100	58	187	210·2
150	28	212	167·9
200	45	190	144·1
250	51	255	192·3
300	8	187	135·5
350	8	58	123·1

A gradient from an area source similar to the above is indicated by Gassner (1916), who trapped uredospores of *Puccinia coronata* at various distances in a north-west direction from an oat field in Uruguay. At 5 m. he found an average of 3·4 spores per unit area, at 100 m. 1·8 spores, and at 670 m. 1·9 spores (Fig. 5 *G*).

Gradients from line or strip sources with particles which are outside the scope of the present review, but apparently compatible with the theory, are to be found in data on dispersal of the fruits of *Leontodon* (*Apargia*) *hispidus* (Brownlee, 1911), and the distribution of atmospheric contamination around Norwich (Brunt, 1932).

V. Discussion

In the theory developed here the dilution of the suspended spore cloud by eddies is regarded as the major factor controlling the deposition gradient, and in this respect the theory differs from the usual treatment (e.g. McCubbin, 1944) by relegating the speed of fall of spores and speed of wind to the role of second-order corrections. Horizontal and vertical dispersal are part of the same diffusion process, and the ultimate vertical gradient depends on turbulence and rate of fall. The theory allows for the deposition of large quantities of spores beneath the pileus of an agaric

(Buller, 1909, p. 217) even in exposed situations, and it may be noted here that the deposition of fungus spores in high concentration on a small area is not necessarily wasteful because the phenomenon of hyphal fusions, which permits the vegetative union of mycelia from different spores of the same species, probably leads to the virtual abolition of intraspecific competition among the higher fungi.

It has been shown that the observed gradients of undoubted wind-dispersed spores are compatible with recent theories of eddy diffusion in the atmosphere, and that data on spores dispersed from a point source are in very close agreement with it. It is not possible to predict the absolute number of lesions from a source, as this must depend on how favourable conditions are for infection, but if the intensity of infection is known in any one position it should become possible to predict the numbers of infections at any other distance over a uniform field. The number of lesions at some standard distance might well be taken as a comparative measure of the totality of factors favouring infection. The limits of spore dispersal are theoretically unbounded until the spores are washed out of the air by rain, but the gradients predicted by this theory are nevertheless steeper than those previously deduced by Schmidt, who believed that one-hundredth of the spores of *Bovista* liberated near the ground would travel more than 460,000 km. Interpolation of the table of Q_x (Appendix) indicated that on the present theory only one-hundredth would travel more than 16 km. under normal conditions of turbulence, and with low turbulence the limits of dispersal would be as low as 50 m. In this connexion it is of interest that Hyde and Williams (1944) as a result of daily trapping of pollen for a year near Cardiff concluded that most of the pollen trapped could have originated within 1000 m., and that very little need have come from more than 10 km. As a practical deduction from this, more reliance can be placed on the effect of spatial separation in protecting clean crops from contamination, but more attention should be paid to eliminating sources of infection within the crop itself. In a comparatively little known paper, Fracker (1936) has studied the influence of the distribution of sources of *Cronartium ribicola* within stands of *Pinus Strobus*, and has obtained a measure of the effect of non-uniform distribution of *Ribes* in relation to the distribution of *Pinus*. It was shown that ecological factors causing aggregation of the *Ribes* resulted in fewer infected trees than would be expected from the same amount of *Ribes* uniformly scattered.

The use hitherto of a double logarithmic scale, although convenient in plotting observations over a large range of concentrations and distances, has obscured the essential feature of the curve. This is better shown in Fig. 6, where Bonde and Schultz's (1943) data for potato blight from Table 10, and the theoretical curve for dispersal from a point source ($m = 1{\cdot}75$) are plotted on an ordinary arithmetical scale. This brings out the fact that for a given interval of distance near the source, the deposition changes much more rapidly than over the same interval in a remote position. The gradient is thus a 'hollow curve'. This may help to explain the two apparently distinct forms in which potato blight may appear on a field: spread from a few foci, or evenly spotted over the field, without

invoking splash dispersal for which there is no evidence in *Phytophthora infestans*. In the former case spread is from sources (not necessarily primary) within the crop and the number of lesions decreases steeply a few yards away from the centre. Where the spots are evenly distributed the field probably lacks foci and is located on the flattened tail of the gradients of one or many distant sources of infection.

The study of disease gradients bears on the design of field experiments with epidemic plant diseases. Current designs for replicated and factorial trials have been developed largely for tests with varieties and fertilizers in which it is fair to assume that, provided narrow guard strips between plots are discarded, the treatment given to one plot does not affect its neighbours. With air-borne organisms attacking the shoot systems of plants this assumption is invalid. For instance, a small plot of potatoes sprayed with a copper fungicide for the control of blight might be exposed to many

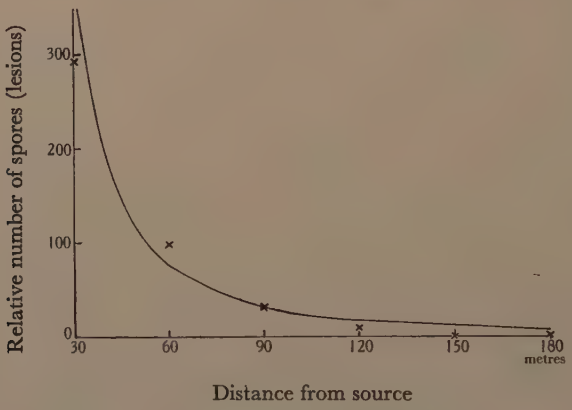

Fig. 6. Expected deposition from a point source (—) plotted on ordinary numerical scale ($m = 1.75$), and observed gradient of potato blight lesions (×) from a point source, Bonde and Schultz's data.

thousands of times the intensity of contamination that it would have experienced if surrounded only by treated plants. The width of guards can be increased only at the cost of increasing error from other causes. One approach to the problem would seem to lie in arranging plots so that the gradient of infection can be taken into the calculation.

The use of gradients as a research tool has already been mentioned in enabling the source of potato-blight outbreaks to be traced by following the gradient to its source. Light may also be thrown on more obscure problems when it is considered that the gradient of passively air-borne spores dealt with in this paper is only one among a number of types of gradient that may be shown by land micro-organisms. The disease gradients due to a fungus extending radially by hyphal growth such as a ringworm lesion on the skin, patches of clover rot (*Sclerotinia trifoliorum*), or tropical species of *Rosellinia* (Nowell, 1923), are exceedingly sharp and characteristic. Slime-spored fungi and most bacterial plant pathogens appear to depend for transport on splashing by raindrops (Faulwetter,

1917; Rolfs, 1942), and this mechanism also plays a part in the dispersal of *Sclerospora* from maize (Weston, 1923). The theory of this dispersal mechanism has not yet been worked out, but from the slight data noted above the gradient appears flatter than that resulting from wind transport alone. This is possibly because, while small water droplets containing spores may themselves be carried like dry spores in the wind, the spore when once deposited on a surface is not permanently out of play but is eligible for a further movement by another rain splash. As Garrett (1943) points out: 'such a mode of dispersal would probably be most effective in increasing the incidence of disease within a crop, but much less effective (than dry air) in transferring it from one crop to another.' The splash mechanism needs special study, both in the open air and under glasshouse conditions where splashing with water may be vigorous.

Still another condition of dispersal obtains when transfer is carried out by insects moving under their own power. The particle dispersed may be a protozoan, pollen grain, fungus spore or virus, but the gradient is likely to be that due to the diffusion of a stationary cloud, not to the wind-blown cloud dealt with in this paper. A study of this mechanism was attempted by Pearson and Blakeman (1906) and by Brownlee (1911), without much progress. Some field data for virus diseases have been given by Frampton and others (1942) and by Bald and Norris (1943). Zentmeyer, Horsfall and Wallace (1943) in their study of Dutch elm disease found that, for the local spread of the slime-spored, insect-borne fungus, *Ceratostomella ulmi*, 'the percentage of trees diseased, plotted as probits, decreased with the logarithm of the distance from a central source of inoculum.' Detailed discussion of these mechanisms must be postponed for the present.

Several kinds of deviation from the theoretical gradients are to be expected. Sampling errors become relatively greater at greater distances, both because of the difficulty of accurately assessing a very low level of infection without taking very large samples, and also because of the comparative rarity of the larger eddies of which a number must have operated before the very distant distribution is smoothed. Given a large number of eddies the dispersion pattern is regular, not in spite of eddies, but because of them. Another source of deviation is the fact that in western Europe and many tropical countries at any rate the uniform topographical field which we have postulated is only realized over very small areas.

Once the general type of gradient has been established for a topographically uniform field it should become possible to study quantitatively the effect of various kinds of natural and artificial barriers, such as screens, intervening crops and topographical features, on the dispersal of spores and pollen (Rempe, 1937; Roemer, 1932; Pope, Simpson & Duncan, 1944).

The dispersal of spores in air is a complex process, and it is not to be expected that the patterns of dispersion would be explained by means of a few aeroplane ascents in North America and Europe, a dozen or so experimental plots in various parts of the world, and two tests on trapping artificially liberated spores in the open air at Leningrad. The formulae provisionally suggested need not therefore be taken too seriously, but the

facts reviewed here indicate that viewed on a logarithmic scale there is an orderliness about the process which was perhaps unexpected, that the range of density of deposition varies with distance from the source within fairly narrow limits, and that out of the multitude of factors affecting the deposition at any distance the strength and the dimensions of the source and the turbulence of the atmosphere are predominant.

This interpretation of observed gradients is suggested tentatively as a first approximation in the hope of evoking more experiments and better field records in this aspect of aerobiology.

Summary

The deposition of air plankton, such as passively air-borne pollen grains or fungus spores, decreases with increasing distance from a source. The factors controlling the scattering of air plankton are reviewed, and observed gradients of deposition are discussed with special reference to fungi causing diseases of plants.

The terminal velocities of spores are shown to depend on their dimensions and to be roughly of the order expected for smooth, spherical particles from Stokes's law, but fairly wide deviations between observed and expected values are believed due to surface roughness and asymmetry. Fungus spores have been observed to fall with velocities between 0·04 and 2·5 cm.sec., and pollen grains between 1·5 and 40 cm.sec. The mean wind velocity at 10 m. is near 300 cm.sec. Attempts to calculate the dispersal of spores as the resultant of vertical fall under gravity and horizontal wind movement are shown to apply only to non-turbulent air movement, and therefore to be inapplicable at heights more than a few millimetres above the earth's surface. Differences in rate of spore fall are probably not major factors in dispersal. It is more appropriate to consider a spore cloud in suspension in the air in process of being diluted by eddies in the course of its transport by the wind.

In support of the concept of the spore cloud as a suspension it is shown that at heights in the atmosphere above the surface layers, the concentrations of pollen and spores decreases exponentially with increasing height in the manner that would be expected if particles falling under gravity were balanced by other particles diffused upwards by eddies. The values for eddy diffusivity, K, varying from $1{\cdot}5 \times 10^4$ to $3{\cdot}3 \times 10^5$, deduced for spores and pollen, are of the order usually found in meteorological work.

While terminal velocity may play only a small part in spore dispersal, it may be more important in causing deposition of spores brought down by eddies to the boundary layer of relatively still air a few centimetres thick at the earth's surface.

The earlier theories of eddy diffusion, including that of Schmidt, are compared with recent work by Sutton who considered that the size of eddies effective in diluting a cloud, instead of remaining constant, increases with the distance travelled by the cloud. Experiments by Stepanov, in which spores were liberated from a point in the open air and trapped at various distances and in different directions, are shown to be in excellent

agreement with Sutton's theory, and to lead to almost identical values for the parameters for diffusion and turbulence with those found by Sutton.

Based on Sutton's theory, equations are given for the deposition of spores at various distances from a point-source, and from Stepanov's data it is concluded that in travelling across 1 sq.cm. of surface there were deposited the equivalent of the number of spores present in a layer on the axis of the cloud about half a millimetre thick. This value is expressed as a coefficient of deposition, p, and it is regarded as a parameter of considerable biological significance.

The relevance of the deposition formula is discussed. Observed gradients of air-borne plant infections originating from a point source are shown to be closely predicted by this theory. Fungi known or suspected of being splash-dispersed on the contrary show gradients incompatible with the theory. Gradients from strip sources cannot be dealt with satisfactorily at present, but an approximate formula is given, and observed gradients from strip sources are found to show reasonable agreement.

The significance for plant hygiene of this interpretation of fungus spore dispersal is that, while attention should be paid to isolation, most emphasis should be placed on eliminating foci of disease within a crop.

This work suggested itself during the course of field studies on potato-virus diseases carried out under the auspices of the Agricultural Research Council. Thanks are offered to my colleagues and correspondents who have been generous with advice and suggestions during the course of the study, and especially to my wife, Margaret F. Gregory, who contributed the Appendix and whose mathematical help has been invaluable. None of these, however, is responsible for the interpretation of the data suggested here.

APPENDIX

(1) *The number (N) of spores in a slice of cloud*

The number of spores in a slice through the spore cloud in the xOy plane 1 cm. thick is found by integrating the number of spores in an annular element of this slice between radii r and $(r+\delta r)$. The limits are from 0 to ∞ as the cloud has no finite boundary:

$$\begin{aligned}
N &= \int_0^\infty \chi 2\pi r\,dr \\
&= \int_0^\infty \frac{2Qe^{-(r^2/C^2x^m)}}{\pi^{\frac{1}{2}}C^3x^{\frac{1}{2}m}}\,2\pi r\,dr \\
&= \frac{2Q}{\pi^{\frac{1}{2}}C^3x^{\frac{1}{2}m}}\int_0^\infty e^{-(r^2/C^2x^m)}\,2r\,dr \\
&= \frac{2Q}{\pi^{\frac{1}{2}}C^3x^{\frac{1}{2}m}}\left[-C^2x^m e^{-(r^2/C^2x^m)}\right]_0^\infty \\
&= \frac{2Q}{\pi^{\frac{1}{2}}Cx^{\frac{1}{2}m}}.
\end{aligned}$$

(2) *Q_x, the quantity of spores in the cloud when its centre has moved a distance x*

Deposition, $$D = pN = \frac{p2Q}{\sqrt{(\pi)}\, Cx^{\frac{1}{2}m}}.$$

Assume the rate of deposit uniform while the cloud moves a distance δx. Then the deposit during this move

$$(-\delta Q) = \frac{p2Q}{\sqrt{(\pi)}\, Cx^{\frac{1}{2}m}} dx,$$

$$\frac{dQ}{Q} = -\frac{2p}{\sqrt{(\pi)}\, C} \frac{dx}{x^{\frac{1}{2}m}}.$$

The solution of this equation is

$$Q_x = Q_0 \exp\left[-\frac{2px^{(1-\frac{1}{2}m)}}{\sqrt{(\pi)}\, C(1-\frac{1}{2}m)}\right].$$

(3) *Deposition down wind (d_w) from a point source at the origin*

Take the x-axis in the direction of the wind and consider a cylinder of unit cross-section around this axis. The number of spores (n_w) passing over the point $(x, 0, 0)$ is the total number in this cylinder. The number of spores in an element of the cylinder length δr is $1\delta r\chi$. Therefore

$$N = \int_{-\infty}^{\infty} 1\, dr\chi$$

$$= \int_{-\infty}^{\infty} \frac{2Qe^{-(r^2/C^2x^m)}\, dr}{\pi^{\frac{1}{2}} C^3 x^{\frac{1}{2}m}}$$

$$= \frac{2Q}{\pi^{\frac{1}{2}} C^3 x^{\frac{1}{2}m}} \int_{-\infty}^{\infty} e^{-(r^2/C^2x^m)}\, dr$$

$$= \frac{2Q}{\pi^{\frac{1}{2}} C^2 x^m} \sqrt{\pi}$$

$$= \frac{2Q}{\pi C^2 x^m},$$

$$d_w = \frac{p2Q}{\pi C^2 x^m}.$$

(4) *Number (d_{lw}) of spores from a line source deposited down wind at right angles to the line only*

The spores are emitted from the y-axis. The number of spores (Q_0) emitted at the point $(0, y, 0)$ passing through an element of volume at a point $P_{(x,0,0)}$ is the same as the number of spores from a puff Q emitted at the origin passing through an element of volume at $(x, y, 0)$. Thus we

can consider each puff as coming from the origin and passing over elements of the strip parallel to Oy through P. The number of spores passing over this strip is that in a slice of cloud Q emitted from the origin and this has already been shown to be

$$\frac{2Q}{\sqrt{(\pi)Cx^{\frac{1}{2}m}}},$$

therefore

$$d_w = \frac{p2Q}{\sqrt{(\pi)Cx^{\frac{1}{2}m}}}.$$

Table 21. *Quantity of spores in the cloud and deposition per unit area*

Calculated for: $Q_0 = 10^{10}$; $C = 0{\cdot}6$; $2p = 0{\cdot}1$

	Distance in cm.									
	10	100	1000	2000	5000	10,000	20,000	50,000	100,000	1,000,000
$\log_{10} x$	1·0000	2·0000	3·0000	3·3010	3·6990	4·0000	4·3010	4·6990	5·0000	6·0000
$\log_{10} Q_x$										
$m = 1{\cdot}75$	9·5761	9·4282	9·2289	—	—	8·9600	—	—	8·5960	8·1070
$m = 1{\cdot}24$	9·7422	9·3816	8·5170	8·1980	7·2660	6·4410	5·3690	3·4400	—	—
$\log_{10} D$										
$m = 1{\cdot}75$	7·6794	6·6615	5·5922	—	—	4·4533	—	—	3·2193	1·8603
$m = 1{\cdot}24$	8·0955	7·1149	5·6303	5·1247	3·9460	2·9343	1·6757	$\bar{1}{\cdot}5000$	—	—
$\log_{10} d$										
$m = 1{\cdot}75$	5·8813	3·8634	1·7941	—	—	$\bar{1}{\cdot}6552$	—	—	$\bar{3}{\cdot}4212$	$\bar{3}{\cdot}0622$
$m = 1{\cdot}24$	6·2974	4·3168	1·8322	1·0256	$\bar{1}{\cdot}4489$	$\bar{2}{\cdot}1362$	$\bar{4}{\cdot}5766$	$\bar{6}{\cdot}0029$	—	—
$\log_{10} d_w$										
$m = 1{\cdot}75$	7·0736	5·1757	3·2264	—	—	1·2075	—	—	$\bar{1}{\cdot}0935$	$\bar{4}{\cdot}8545$
$m = 1{\cdot}24$	7·7497	6·1491	4·0445	3·3523	1·9267	0·7285	$\bar{1}{\cdot}2833$	$\bar{4}{\cdot}8607$	—	—

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ANNUAL GENERAL MEETING

9 December 1944

The Annual General Meeting for 1944 was held in the Department of Biology, Chelsea Polytechnic, London, on Saturday, 9 December, with the President, Mr R. W. Marsh, in the Chair.

After the Minutes of the last Annual Meeting had been read and signed, the President announced with deep regret the deaths of six members: Miss D. Ashworth, Prof. A. H. R. Buller, Miss C. A. Cooper, Mr R. A. Findlayson (who died in 1943), Mr A. W. Oke, and Mr A. Wallis.

Reviewing the past year the President recalled that the East Malling meeting had to be cancelled, but that the other meetings and a successful series of day forays had been held as arranged. He announced that the Council had, that morning, established a permanent Foray Committee of four members (one to retire each year) together with the Secretary *ex officio*, to organize the Society's field activities. He drew attention to the publication of the third edition of the *List of Common Names of British Plant Diseases* under the new title of *List of Common British Plant Diseases* (a copy of which had been sent to every member), expressing the Society's thanks to the Agricultural Research Council for a grant of £100 towards the cost of publication and to Mr W. C. Moore and Dr G. R. Bisby for editing this co-operative work and seeing it through the press. He also reported that in June a Sub-committee consisting of K. St G. Cartwright, R. V. Harris, W. C. Moore (*Chairman*), G. Smith, Miss E. M. Wakefield (*Secretary*), and the President and Secretaries *ex officio*, which had been appointed by the Council in October 1942 to investigate the present state of systematic mycology in this country and the part the Society might play in its development, presented a comprehensive report to the Council. The Council decided that the report should not be published at present, but it has been printed and copies have been sent to all Universities, Government Departments, Institutes, and Associations concerned with the activities of fungi. Attention was also drawn to the collection of surplus reprints on mycology and plant pathology for war-damaged libraries which the Society was organizing.

After the year's Accounts had been submitted by the Treasurer, Mr A. A. Pearson, and adopted, the following Officers and Councillors for 1945 were elected: *President*, G. Smith, M.Sc.; *Vice-Presidents*, Mrs E. W. Mason and the two past-presidents, R. W. Marsh and S. P. Wiltshire; *General Secretary*, J. Ramsbottom; *Secretary*, G. C. Ainsworth; *Treasurer*, A. A. Pearson; *Editors*, B. Barnes and H. Wormald; *Councillors*, R. W. G. Dennis, C. G. Dobbs, and G. Samuel (to replace S. D. Garrett, Mrs E. W. Mason and A. Smith). The Plant Pathology Committee's nominations of H. E. Croxall, W. C. Moore and E. R. Wallace (to replace W. Buddin, W. R. Day and A. Smith) were agreed to. Six new members were elected, making twenty-two for the year.

The changes in the Rules which had been proposed by the Council so that the Society could accept Associates were then discussed and it was unanimously agreed that:

Rule 4 shall be deleted and that Rules 2 and 11 shall read:

2. The Society shall consist of Honorary Members, Members (including Foundation Members*), and Associates; the number of Honorary Members shall be limited to 20 at any one time but the numbers of Members and Associates shall be unlimited.

*Foundation Members are those Members or Societies who joined the Society previous to the limit of 100 Members having been attained. This was reached 22 October 1903.

11. The Society shall hold one or more meetings annually at a place and time determined by the Members at the preceding Annual General Meeting, or by the Council.

and that this new Rule be inserted after Rule 10:

All Associates shall be proposed by two Members. They shall be elected by a majority of the Members present at a meeting of the Society and shall pay an annual subscription of five shillings. They shall be eligible to attend the Society's meetings and forays but not to vote at any meetings or to receive the *Transactions*.

After discussing the programme for 1945 the meeting adjourned until 2 o'clock when the President delivered his address entitled 'Mycological Contacts'. A vote of thanks to Mr Marsh concluded the meeting.

G. C. AINSWORTH
Secretary

RECEIPTS AND PAYMENTS

for the year ending 30 June 1944

		£	s.	d.
1943				
1 July	Balance brought forward ...	240	8	11
4 Aug.	Grant from Royal Society ...	100	0	0
1944				
22 March	Grant from Agric. Research Council	100	0	0
3 May	Sale of *Transactions*:			
	Current Volume	104	14	0
	Back Volumes	71	5	8
	Sale of Reprints	5	7	10
	Sale of *British Basidiomycetae* ...	4	8	7
	Diseases of British Grasses ...	2	13	3
30 June	Subscriptions to date ...	335	2	4
	Gifts to Printing Fund ...	4	0	0
	Deposit Interest	1	0	0
	War Loans Interest	25	14	4
		£994	14	11

		£	s.	d.
1944				
3 May	Cambridge University Press: Cost of Vol. XXVI *Transactions* and Reprints ...	421	0	6
30 June	Postages, etc.			
	Treasurer	3	0	0
	Secretary	11	11	5
	Sec. Path. Committee ...	1	9	0
	Editor	1	17	7
	Sundry Printing	10	13	6
	Fees of Meetings	3	19	6
	Purchase of *Transactions* ...	8	2	6
	Honorarium to Miss Kierans	4	4	0
	Photograph of Berkeley Portrait	2	13	0
	Balance in bank	526	3	11
		£994	14	11

CAPITAL ACCOUNT—*Robinson Bequest* £50, *Cheesman Fund* £150, *Printing Fund* £500 } *invested in* £255 3½ % *War Stock.* £245 3½ % *War Loan.* £200 3 % *Defence Bonds.*

A. A. PEARSON, Hon. Treasurer

Examined and found correct, E. W. SWANTON

FORAYS, 1944

A spring foray was held at Ruislip woods on 20 May, and a series of day forays was arranged for the autumn on the same lines as in 1943. The Glasgow and Andersonian Natural History and Microscopical Society (9, 16, 30 Sept., 7 Oct.), the Haslemere Natural History Society (16 Sept.), the Yorkshire Naturalists' Union (22–26 Sept.), the Norfolk and Norwich Naturalists' Society (28 Sept., 8, 21–22 Oct.), the Bournemouth Natural Science Society (5, 26 Oct.), the Leicester Literary and Philosophical Society (Botany and Biology Section) (7 Oct.), and the Lincoln Naturalists' Union kindly invited members to attend their forays. Joint forays were held with the Hertfordshire Natural History Society (16 Sept.), the Chingford Branch (23 Sept.) and the Ecological Section (29 Oct.) of the London Natural History Society, the South London Botanical Institute (Oxshott, 7 Oct.), and the Maidstone Scientific and Antiquarian Society (East Malling, 21 Oct.), while Ruislip woods (1 Oct.) and Englefield Green (14 Oct.) were again visited by the Society.

At the first of the joint forays, a large party visited Whippendell woods near Watford where the commoner species were found to be in good variety. In Epping Forest on 23 Sept. the Society began a census of the fungi in the Cuckoo Pits area where the Chingford Branch of the London Natural History Society are making a detailed ecological survey and later in the season assistance was also given to the Ecological Section of the same Society with its Bookham Common survey. Ruislip woods again provided a rich harvest when Mad Bess wood was worked this year for the first time. Among the finds was *Boletus cramesinus* Secr. (=*B. sanguineus* Wither. ex Fr. var. *gentilis* Quél.) (specimens of which have been deposited in the Kew Herbarium), for which there appears to be no published British record, although it was found by E. W. Swanton and A. A. Pearson at Shillinglee Park, Sussex, in 1943; and two very large sporophores of *Psalliota augusta* from a nearby allotment attracted attention. The Englefield Green foray added further records to those of previous years for the Clockcase plantation, and at East Malling specimens of over 100 species were laid out in the laboratories of the Research Station to which the Society was indebted for hospitality. A feature of the latter foray was an interesting collection of species of *Clavaria* comprising *C. cinerea*, *C. corniculata*, *C. cristata*, *C. inaequalis*, *C. Kunzei*, *C. rugosa*, and *C. stricta*.

The Forge Valley area covered by the Yorkshire Naturalists was good fungus country and nearly 250 species were recorded. Yelmandale and Bedale woods and the Raincliffe woods were visited and some interesting associations were noted by Miss Grainger. *Hygrophorus eburneus*, dominant on the dry limestone slopes under beech, was associated with several species of *Cortinarius*, e.g. *C. purpurascens* and *C. testaceus*. *Psalliota xanthoderma* var. *obscurata* Maire was found in pastures near Ayton. (There is no published record of this fungus in Britain although it has been gathered in the southern counties.) *Lactarius deliciosus* and *Lycoperdon depressum* were abundant in the spruce plantings in Raincliffe wood. On the Saturday, Mr A. A. Pearson, Chairman of the Mycological Committee of the Y.N.U., gave an address on 'The study of agarics'.

The last foray of the season was the joint one with the London Natural History Society to Bookham Common where a survey of the flora and fauna was begun in 1941. As a result of this year's visit the list of the fungi of this area was increased to 180 species. The woods are mainly oak and the only specimen of *Amanita muscaria* found was under a solitary birch.

UNA C. MASON
Secretary of the Foray Committee

PROCEEDINGS

Meeting held in the English Lecture Theatre, the University, Edmund Street, Birmingham, 28 October 1944. The President, R. W. Marsh, M.A., in the Chair.

Seed-borne fungi

A. SMITH. Seed examination at the Plant Pathology Laboratory, Harpenden.
Miss MARY NOBLE. *Phialea temulenta*—the Blind Seed fungus.
Miss K. SAMPSON. Some endophytic fungi of grasses.
W. A. MILLARD. Broccoli Canker.
L. G. G. WARNE. A seed-borne outbreak of Club Root.
G. C. AINSWORTH. The geographical distribution of some seed-borne fungi.

General Discussion. [For a summary of this discussion, see *Nature, Lond.*, CLV (3924), 36–7, 1945.]